FINAL REPORT

HISTORIC RANGE OF VARIABILITY OF PIÑON-JUNIPER WOODLANDS ON THE UNCOMPAHGRE PLATEAU, WESTERN COLORADO

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SUMMARY

This study describes the current range of structural variability of piñon-juniper woodlands on the Uncompahgre Plateau by synthesizing the results of four case studies carried out between 2000 and 2003. Current and historic ranges of variability were investigated through intensive field studies that used tree-rings to reconstruct portions of the pre-1880s landscape and related disturbance processes.

In general, piñon-juniper woodland stands were much older than expected, ranging from 40 to 700 years. A pulse of new stands as well as recruitment of trees into existing stands occurred within a few decades of the introduction of livestock in 1881. However, the majority of stands were significantly older than this. Comparison of the number of trees establishing in the early 1900s to previous periods shows increasing density that began 250 years ago, with an earlier wave beginning about 550 years ago. Also, many older stands are dominated by large juniper trees, which suggest that insect outbreaks or other disturbance that selectively cause the death of piñon pine trees operated periodically in the past. Structural evidence and tree growth-indices from multiple sites suggest that climate drives cycles of tree establishment and mortality in woodlands.

This study found no evidence to support the assumption that frequent, low intensity fires commonly occurred in any part of the piñon-juniper zone. Instead, the current evidence suggests that woodlands in the upper piñon-juniper zone generally initiate following infrequent, stand-replacing fires. Fire intervals may be 200-1000 years. Between fires, other dynamic processes control stand structure. Lower elevation woodlands, with either low productivity or a small-statured, brushy understory may burn infrequently in high severity fires, but appear to be controlled primarily by soil moisture. Therefore, this study concludes that the current fire potential is not outside of the historic range of variability for woodlands. High-severity fires occurred in the past and can be expected to continue to occur.

Taken together, the evidence strongly suggests that an aging woodland landscape is not outside of the natural range of variability for Uncompahgre Plateau woodlands. Old-growth stands were a common component of the pre-settlement landscape. The frequency of old-growth stands and ubiquitous evidence for infrequent, stand-replacing fires and periodic disturbance selective to piñon pine indicates that the distribution of seral stages comprising the landscape mosaic may fluctuate dramatically from century to century. While changes to some woodlands and shrublands have occurred since the introduction of livestock, these changes do not appear to depart from the long-term dynamics of woodlands on the Uncompahgre Plateau when considered on a landscape scale.

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INTRODUCTION

Throughout the western United States there is growing consensus that native ecosystems are in poor health because of fire suppression and historic management practices. Unfortunately, blanket statements about forest health and fire regimes, such as the recent Healthy Forests Initiative (U.S. Government 2003), make little distinction among different types of forest, similar forests in different topographic positions, or similar forests in different regions. Fuel accumulations and fire regimes vary under all of these circumstances and in response to climate patterns, though generalizations can be made for each case where enough local information has been collected (e.g., Southwestern U.S.: Swetnam and Baisan1996). One major concern in the West is that forests have missed several fire cycles resulting in an unnatural buildup of fuels (Covington and Moore 1994, Moore et al. 1999). However, researchers in the Southwest and other regions have found that prior to c. 1900, even fire-adapted ponderosa pine forests experienced periods without fire or may naturally experience high-intensity, stand-replacing fires (Veblen and Lorenz 1986, Shinneman and Baker 1997; Brown et al 1999; Veblen et al 2000; Kaufmann et al 2000; Brown and Sheppard 2001). The bottom line from a wide variety of fire history studies in different places and forest types is that disturbance regimes vary from region to region and are dynamic in time, varying in response to short- and long-term climate cycles. Thus, restoration programs should not only consider the vegetation type and its local variation, but also how climate patterns have influenced past community dynamics and disturbance propagation through space and time (Veblen 2003). Both rare and common events in the distant past have left ecological legacies that continue to influence community composition, productivity and disturbance regimes (Magnuson 1990). Without some understanding of this pre-historic variation in a particular system we have little hope for altering modern landscapes in order to meet the goals of ecological restoration. Recognition of spatial and temporal variations in geographic space cautions us to

investigate assumptions about ecological integrity prior to applying restoration treatments over a broad area.

Two general assumptions of the Healthy Forests Initiative are: 1) forests are degraded and in need of restoration and 2) fire regimes have switched from frequent, low-intensity fires to infrequent, high-intensity fires (U.S. Government 2003). In response, fuel reduction programs are promoted as an answer to the dual needs of both fire mitigation and ecosystem restoration. However, restoration and fire mitigation may often be incompatible goals (Veblen 2003, Romme et al 2003). For some land uses and types, such as utility corridors, reservoir protection, or the Wildland-Urban Interface, fire mitigation and public safety are primary management concerns and restoration is a secondary goal. In these cases, especially where catastrophic fires are likely, fuels reduction may have a higher social priority than restoration. In less sensitive areas, though, restoration is often cited as justification for fuels reduction even when the local fire regime has not been investigated.

One example where this viewpoint applies is piñon-juniper woodlands on the Uncompahgre Plateau. Restoration plans for the Uncompahgre Plateau assume that the extent of piñon-juniper has increased since cattle were introduced in 1880 (Uncompahgre Plateau Partners 2003). According to this scenario, grazing caused the deterioration of rangelands by excluding fire through reduction of fine fuels, and also reduced grass competition with tree seedlings. If true, grazing may have facilitated tree- and shrub- invasion into rangeland as well as increasing tree densities in existing savannas. Prior to grazing, the woodland-grassland matrix was thought to comprise mostly early to mid-seral patches that were maintained by frequent, low-intensity fires. Old-growth woodlands were restricted to places where productivity was too low to maintain horizontal connectivity of fuels. If these assumptions hold, increased tree density and conversion to woodlands since Euro-settlement can be cited as evidence that the landscape is over-mature with more horizontal and vertical connection of fuels, and hence increased risks for larger, more intense fires than would naturally occur. In that case, assumptions justify plans to restore the balance of the landscape to earlier seral-stages that will "sustain frequent, low-intensity fires that burned they way [they] used to" (Uncompahgre Plateau Fire Plan 1999). If not true, restoration attempts may

adversely affect a large fraction of the landscape – piñon-juniper covers more than one third of 1.6 million acres on the Uncompahgre Plateau (Uncompahgre Plateau Partners 2003). Examination of assumptions is essential prior to implementation of restoration treatments.

One way to test assumptions about natural dynamics of an ecosystem is to investigate its historic (or natural) range of variability (Landres et al 1999, Swetnam et al 1999). Some key characteristics used to define the range of variability for wooded ecosystems are species composition, tree sizes and ages, and disturbance regimes (Swanson et al. 1993; Kipfmueller and Swetnam 2001). Interest in range of variability has evolved from the idea of ecosystem management, where landscapes are managed as integrated wholes instead of patches of land defined by political and/or project boundaries. Ecosystem management asserts that native ecosystems evolved under some regime of climate variability and natural disturbance, and continue to operate within these contexts as well as those imposed by anthropogenic influences (Swanson et al. 1993, Humphries and Bourgeron 2001). Comparing current conditions and processes to those that were present for some period of time prior to Euro-settlement can indicate whether a system is operating within the environmental context under which it evolved, or whether the system has moved away from the historic range of variability. Movement outside of the natural range of variability may lower its resilience to future disturbance and may irreversibly shift the system to a new successional trajectory (Holling and Meffe 1996). Thus, in addition to testing assumptions about historic dynamics, a range-of-variability study might also identify parts of the system that are most vulnerable to change or those that are most in need of repair. It might also suggest alternative goals for fuels mitigation projects that can better maintain ecological integrity.

This study describes the current range of variability of piñon-juniper woodlands on the Uncompahgre Plateau by synthesizing the results of 4 case studies carried out between 2000 and 2003. Current and historic ranges of variability were investigated through intensive field studies that used tree-rings to reconstruct portions of the pre-1880s landscape and related disturbance processes. Prior to the current study, best management practices were forced to rely on assumptions and expert opinion derived

from studies outside the local region. Thus, the first part of this report reviews the state of knowledge available from the piñon-juniper literature. The next part introduces the study area, methods, and results from the case studies. The final section interprets the results and discusses implications for restoration and fuels management.

REVIEW OF THE PRESENT STATE-OF-KNOWLEDGE

Ecology of Piñon-Juniper Woodland Ecosystems

Piñon-juniper woodlands are widely distributed throughout the western U.S., where they often comprise the lower tree line. In western Colorado on the Uncompahgre Plateau they are generally found between 1800 and 2800 meters elevation. The majority of woodland trees are of low stature -- under 10 meters, and often much less than this. The tree canopy is patchily distributed, generally comprising less than 50% cover. All piñon-juniper woodlands are similar in that they are composed of some combination of piñon pine and/or juniper species, usually one of each. For example, *Pinus monophylla* (single-needle piñon) occurs in the Great Basin and on the western Colorado Plateau, whereas *P. edulis* (Colorado piñon) occurs to the east of the range of *P. monophylla* in eastern Utah, Colorado, Arizona and New Mexico. Throughout their range, piñon pine trees tend to dominate the higher elevation part of the woodland zone while juniper dominates lower elevations.

The combination of piñon pine and juniper species at any site is controlled by regional and local climate regimes (Neilson 1987). In a particular region, the combination of tree species has not changed much over the last several centuries; however, the physical appearance and proportions of each species may have changed dramatically over this same time period. It is likely, given the extensive range of woodlands over several distinctive climate regions and the different mix of species from region to region, that ecology and disturbance regimes vary geographically and have been affected by climate change and settlement in different ways. There is variation from region to region, but probably also local variation that is determined by differences in elevation, aspect, substrate, and accessibility. However, when describing piñon-

juniper, many authors commonly make no distinction between woodlands that occur in the Great Basin, Colorado Plateau, the Southwest, the Mexican borderlands, or the Front Range of the southern Rocky Mountains. Failure to distinguish between regions obscures important ecological differences from site to site and region to region.

Incomplete knowledge of woodland dynamics and life histories of the tree species further exacerbate the problem of not distinguishing among woodlands from different regions. Many studies interchange species, and even genera, when describing life-history traits. For example, many authors cite studies of juniper-only woodlands to support piñon-juniper invasion throughout the woodland range. The following papers limit their focus to juniper species, but are frequently cited with reference to piñon-juniper woodlands: *Juniperus osteosperma* in southwest Utah (Cottam and Stewart 1940) and in northeast Utah (Barney and Frischknect 1974); *J. occidentalis* in southwest Idaho (Burkhardt and Tisdale 1976) and in eastern Oregon (Miller and Rose 1995, Miller and Wigand 1994); and *J. monosperma* in northern Arizona (Johnsen 1962). Conclusions from these studies tend to be extrapolated and broadly applied to studies where little to no previous data exists, and the ideas are often not tested for their applicability to the more distant sites.

Several studies have focused on early, post-fire succession of the woodland understory (e.g., Great Basin: Barney & Frischknect 1974; Evans 1988; Koniak 1985; Tausch & West 1988; West & Van Pelt 1987; western Colorado: Erdman 1969; the Southwest: Springfield 1976), but few studies have investigated regeneration strategies of piñon pines (Floyd 1981; reviewed in Chambers et al. 1999). One study of *P. edulis,* from northern Arizona, reported that artificially shading seedlings facilitated seedling survival (Meagher 1943), though a different study of natural seedlings in northern Arizona found that those growing in the interspace between trees were larger with more lateral root development (Harrington 1987) . In comparison, natural seedlings of *P. monophylla* in Nevada were found to be more numerous within the dripline of tree canopies (Everett et al. 1986). Other studies agree that *P. monophylla* in the Great Basin is facilitated by nurse shrubs (Bradley et al. 1992, Chambers 2001), as is *P. edulis* in Utah (Bradley et al. 1992) and western Colorado (Floyd 1982). On the Uncompahgre Plateau, *P. edulis* appears to benefit from both biotic and abiotic shading

by rocks, logs, or other debris, though seedlings can sometimes be found in the open with no obvious source of shade (personal observation).

Some researchers have suggested that high recruitment rates occur when several years of favorable weather follow regional masting events (Arnold et al. 1964; Barney & Frischknect 1974). Masting occurs approximately every 5 to 6 years for *P. edulis* trees (Betancourt et al 1993). Harrington (1987) found a larger number of *P. edulis* seedlings in interspaces after a good seed year in 1986. A study from Mesa Verde National Park in western Colorado, however, reported no significant change in seedling densities measured annually from 1975-1995 (Floyd et al. 1993). Increases in tree recruitment, therefore, may be associated with a spate of favorable weather, since it appears that the number of piñon pine seedlings remains stable from year to year. Everett et al. (1986) suggested that *P. monophylla* seedlings growing under tree canopies do not contribute to stand dynamics because the longevity of canopy trees keeps them from surviving. In closed woodlands, then, seedlings may be part of an ephemeral understory (*sensu* Oliver 1996) where numerous seedlings establish from year to year, but few survive because of suppression, or unless specific environmental conditions are met (Floyd 1981).

On the Uncompahgre Plateau, seedlings grow very slowly until they overtop their shade source, after which they may continue to grow slowly if suppressed by a canopy, or may grow very rapidly in the open (Fig. 1). This implies that canopy removal can release seedlings that have already established. Non-human mechanisms of canopy removal occur through drought-related mortality, selective disturbance agents such as insects and disease, and old-age senescence. Overall, there is a lack of research describing regeneration dynamics of woodland tree species.

Woodland Succession

Several authors have proposed successional models for piñon-juniper woodlands. A typical model portrays post-fire development from grassland to climax stand (e.g., Arnold et al. 1964). The initial stage is bare ground and skeleton trees followed sequentially by annual plants, annual and perennial forbs, perennial forbs-grasses-half shrubs, then by shrubs, and ultimately culminates into climax piñon-juniper
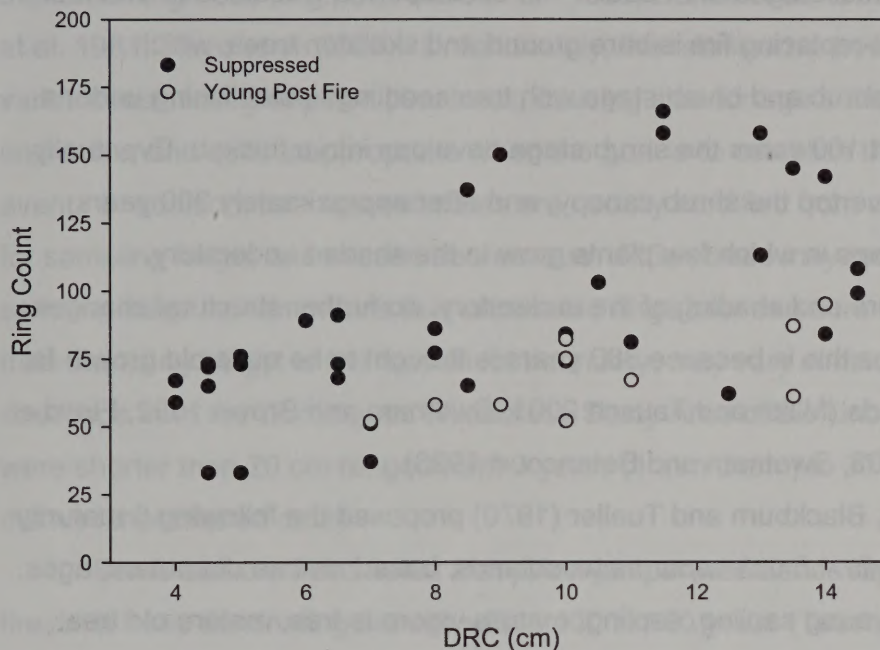
Figure 1. Tree age and diameter at the root collar (DRC) for piñon pine saplings from an open, post-fire site versus saplings suppressed under a closed canopy. Note that similar-sized trees under the canopy can be considerably older than those grown in the open.

woodlands. Pre-historically, fire was thought most likely to occur during the shrub stage or earlier, thus returning the landscape to a state of early succession. Grazing by livestock is generally believed to reduce fine fuels, which decreases the risk of fire. Ubiquitous exclusion of fire throughout Western rangelands appears to have favored the survival of woody species, and subsequently to have caused an increase in the range and extent of many kinds of shrublands and woodlands (Scholes and Archer 1997, McPherson 1997). Under this scenario, one would expect that if fire did pre-historically control the invasion of piñon-juniper trees into grasslands, then much of the landscape would have been maintained in an early seral condition. Indeed, this assumption has driven much of the research efforts in piñon-juniper over the last 50 or more years. In a review of piñon-juniper studies, Miller and Tausch (2001) report that more than 90% of Great Basin woodland trees established after 1860.

Typically, models of post-fire development for piñon-juniper sites do not include a sequence of structural changes that occur once trees have entered the site, though two studies have explicitly addressed stages of development in woodlands. Erdman (1969)

proposed 4 developmental stages of *P. edulis* – *J. osteosperma* woodlands. The first stage that follows stand-replacing fire is bare ground and skeleton trees, which develops into an open shrub and brush stage with tree seedlings establishing under a shrub canopy. At about 100 years the shrub stage develops into a thicket. Eventually, in a third stage, trees overtop the shrub canopy, and after approximately 300 years climax woodland develops in which few plants grow in the shaded understory. Following canopy closure and shading of the understory, no further structural changes are addressed. Perhaps this is because 300 years is thought to be quite old growth for the majority of woodlands (Miller and Tausch 2001, Swetnam and Brown 1992, Floyd et al 2000, Floyd et al 2003, Swetnam and Betancourt 1998).

In another study, Blackburn and Tueller (1970) proposed the following 6 maturity classes for *P. monophylla* - *J. osteosperma* woodlands, based on tree diameters, ages, and heights: seedling, young sapling, sapling, mature vigorous tree, mature old tree, and decadent tree. Size-age-form classes were enumerated in five density classes: open, dispersed, scattered, dense, and closed woodlands. Woody establishment and survival were generally attributed to reduction in fires caused by grazing since the turn of the twentieth century. The oldest (closed) stands initiated prior to 1700. As with Erdman (1969), the authors explicitly include developmental stages in their study, but do not consider stand structures for stands older than 300. Also, it is unfortunate that the authors label the oldest trees "decadent", since Blackburn and Tueller's system has frequently been used to classify piñon and juniper trees. Both species are able to attain ages much older than 300 years, and piñon pine does not show an obligate growth reduction with age (personal observation). In fact, old trees (200++ years) retain their ability to release dramatically. As mentioned above, the decadent label probably arose because many perceive trees > 300 years to be unusual.

Few published studies of piñon-juniper woodlands have used tree-rings to study the long-term dynamics of piñon woodlands. Instead, many studies have relied on either (1) size-age-form class (*sensu* Blackburn & Tueller 1970) to infer stage of stand development or to divide trees into pre- or post-settlement (i.e., Tausch et al. 1981; Waichler 1998), or (2) have aged selected trees within a stand, and then developed a regression coefficient that relates tree size to tree age and then used this model to date

the remaining trees (e.g., St. Andre et al. 1965; Daniel et al. 1966; Floyd 1981; Tausch et al. 1981; Floyd et al. 2000). Unfortunately, the relationship between age and size varies considerably in piñon pine trees, causing size-for-age substitutions to be quite imprecise; and quite inappropriate when the goal is to establish the date of a specific event. In addition, tree age estimates are usually modified from counts by corrections for sampling height and missed tree centers. Piñon trees may grow very slowly at the seedling stage, which means that uncounted rings between core center and pith, or from sampling height to the root-shoot boundary, may vary considerably. For example, seedlings from the Dominguez Wilderness Study Area of the Uncompahgre Plateau that were shorter than 20 cm ranged from 3 years (1 mm diam.) to 30 years old (9 mm diam.) (unpublished data).

Some authors have noted that piñon-juniper woodlands rapidly re-establish after fire, with trees dominating the site within 100 to 150 years (Tausch and West 1988). This rate of establishment is not rapid when compared to rates of post-fire establishment in many fire-adapted forests, so an actual post-fire 'cohort' is difficult to identify. For piñon-juniper, in-filling may occur over an extended period of decades to more than a century. In some cases, trees may fail to re-establish following a stand-replacing fire (Floyd et al 2000). This is a puzzling phenomenon, given the ubiquity of dense thickets of trees frequently reported for the piñon-juniper zone. One outstanding question, then, is whether rates of woodland establishment follow a typical pattern on certain sites, or if the potential for establishment changes through time according to fluctuations in weather. If weather is responsible, one might expect to find pulses of piñon-juniper establishment throughout a region during periods when more soil moisture is available for tree growth. Over 4 years of research, tree seedlings on the Uncompahgre Plateau were fairly abundant in many woodlands, suggesting that woodland initiation is not limited by seed source (unpublished data).

Causes of Vegetation Change in Piñon-Juniper Ecosystem

Fire

Disturbance has been defined as any relatively discrete disruption of the structure of a population, community or ecosystem (White and Pickett 1985). Fire has

long been believed to be the most important disturbance to piñon-juniper. It is frequently implicated as an important control of woodland distribution during pre-historic times (Wright & Bailey 1982). A mean fire return interval of approximately 30 years was suggested as the historical mechanism for maintaining grasslands prior to the introduction of livestock (Leopold 1924). This 30 year interval can only refer to fire frequency near the grassland/woodland ecotone, since mature woodlands found at higher elevations would likely have burned catastrophically (Gottfried et al. 1995).

Unfortunately, woodland fire regimes are hard to document because piñon pine trees rarely scar and are usually killed by fire (Gottfried et al. 1995). Occurrence of fire scars have sometimes been reported, but are often not cross-dated so it is difficult to know if scars represent single-tree burns, small fires, or large fires (Baker and Shinnemen 2004). Attempts to determine fire intervals at the upper ecotone have been made using fire scars collected from ponderosa pine (*Pinus ponderosa*) or Douglas fir (*Pseudotsuga menzeizii*) trees where these forests interdigitate with piñon-juniper woodlands (Erdman 1969; Allen 1989; Despain and Mosley 1990 *in* Gottfried et al. 1995; Swetnam & Baisan 1996). However, the existence of an ecotone suggests that there is ultimately some factor(s) that changes to favor another vegetation type. For this reason, fire interval data collected at ecotones may not be indicative of dynamics in the stable piñon-juniper zone.

Studies from Mesa Verde National Park, in southwest Colorado, suggest that piñon-juniper fire regimes are dominated by infrequent, stand-replacing fire (Floyd et al 2000, Floyd et al 2003, Romme et al 2003). They suggest that typical fire return intervals are about 400 years (Floyd et al 2000). Studies in other regions have also reported evidence for stand-replacing fires (reviewed in Baker and Shinneman 2003). Reports of surface fires and fire-scarred piñon pine or juniper are few, with the majority of studies from the upper ecotone or juniper-only woodlands. Romme et al (2003) report no fire scars found on piñon pine or juniper trees in nearly 10 years of searching and research. Given the lack of documentation of frequent surface fires and the difficulty of getting prescribed fires to burn in piñon-juniper outside of the typical fire season, frequent, low-intensity fire regimes may be far less common than previously has been assumed (Baker and Shinneman 2003). Romme et al (2003) hypothesized that fire

regimes vary in contrasting types of piñon-juniper communities (Table 1). They suggest that only piñon-juniper savannas and shrublands are in need of restoration because piñon-juniper forests have not been significantly altered since the introduction of livestock.

Table 1. Hypothesized piñon-juniper communities and fire regimes (adapted from Romme et al 2003).

Piñon-Juniper Community	Soil Characteristics	Fire Frequency	Fire Severity
Savanna	Deep, fine-textured	Frequent	Low-severity
Shrub-Woodlands	Deep fine-textured	Moderate Frequency	High-severity
Forest	Shallow, rocky or coarse-textured	Very Infrequent	Very High-severity

Drought and Insects

Though fire has been emphasized as the primary control of piñon-juniper structure, other phenomena also impact woodland dynamics. For example, prolonged drought might act to either decrease woodland extent directly through mortality of tree and shrub species (Betancourt et al. 1993, Swetnam & Betancourt 1998), or increase woodland extent through differential mortality of competitors (Allen & Breshears 1998). In either case, the effects of drought become immediately evident, while the ensuing re-establishment of trees may not be apparent for decades. Some studies have suggested that lack of old piñon pine trees in the Southwest may be due to extreme drought that occurred in the late 1500s (Betancourt et al 1993; Swetnam et al 1999; Swetnam and Betancourt 1998, Swetnam and Brown 1992). A 2129-year-long reconstruction of summer precipitation from tree-rings in northwest New Mexico suggested that 1566-1608 was the most severe, short-term period of below-normal precipitation. Other short-term periods of below-normal rainfall in northwestern New Mexico occurred from 1727-1742 and 1899-1904. The reconstruction also suggests that the last 200 years has been unusually wet when compared to the previous 1100 years (Grissino-Mayer

1995). When compared to the entire reconstructed record, above-normal precipitation occurred during 1790-1810, 1830-1880, 1910-1950, and 1970-1990.

In addition to the possibility that drought directly causes mortality of trees, drought may also bring about mortality indirectly by causing stress, which makes trees more susceptible to a host of insects, diseases and parasites (Rogers 1993). Under so-called normal conditions, many kinds of insects use trees as hosts (Leatherman and Kondratieff 2003). Several of these insects may increase during drought, particularly the piñon ips, *Ips confuses*, and the piñon needle scale, *Matsococcus acalyptus* (Leatheman and Kondratieff 2003). The piñon *Ips*, along with twig borers, vector blue-stain fungus, which facilitates successful beetle attack and ultimately causes the death of the tree. Piñon *Ips* attack can be visually identified by the accumulations of boring dust around exit holes and the base of the tree. This evidence is only apparent during the first year or two following tree death when orange needles still cling to the tree. The blue stain can only enter the sapwood while the tree is alive and thus may possibly be used to identify beetle-associated mortality to piñon trees. Though few published studies address the importance of insect-related mortality in piñon-juniper ecosystems, a drought currently under way has brought about the deaths of a great number of piñon pine trees, from small patches to entire hillsides. Mortality is opening up the canopies of woodlands and shrublands and may have dramatic and long-lasting consequences for many plant, animal, and human communities.

Anthropogenic Change

Prior to settlement by Euro-Americans, Ute Indians lived on the Uncompahgre Plateau (Reed and Metcalf 1999). Little is known about how they used the piñon-juniper woodlands. Generally, they traveled in small groups, and did not build permanent structures (Reed and Metcalf 1999). They collected and stored piñon nuts as a source of food, and hunted in and near the woodlands. Horses were acquired around 1650, which probably changed movement patterns. Utes practiced seasonal transhumance, opportunistically following availability of plant and animal food supplies. Winter camps are sometimes associated with piñon-juniper (Reed and Metcalf 1999), where woody debris would have been collected to use for cooking and campfires. Because of the

difficulty of felling trees with crude hand tools, they probably used wood that could be collected from the ground or broken easily from living trees[1]. Charcoal in hearths came from both piñon pine and juniper wood[2], suggesting that coarse woody fuels were locally abundant.

European settlers quickly populated the Uncompahgre Valley in 1881 following the forced removal of the Ute Indians to reservations in Utah (Marshall 1979). Cattle were introduced immediately and early reports suggest that livestock numbers were maintained at very high densities for several decades (Uncompahgre Plateau Partners 2003). Besides rangeland, other uses of the woodlands were for firewood and fence posts. Several roads that cross the Uncompahgre Plateau also date from this early time and adjacent woodlands may have seen heavier use. Wood was used for heat and cooking well into the twentieth century.[3] Collection of firewood was time-consuming but free, whereas coal cost money. Newcomers settled on both sides of the Uncompahgre Plateau, but populations on the west side went through periods of boom and bust from 1930-1980 associated with mining on the northwest end (Uncompahgre Plateau Partners 2003). In addition to disturbance near mines, this increased population put pressure on woodlands through changes to wildlife populations and woodcutting. Woodland impacts were probably most intense close to towns. To this day it is difficult to travel through the woodlands on the Uncompahgre Plateau without encountering old jeep trails and stumps, cut trees, or salvaged logs (personal observation).

Anthropogenic influences that may have affected woodlands since settlement by Euro-Americans are grazing by livestock, fire suppression and/or interruption of the fire regime, mechanical eradication of woodlands and woodcutting, seeding of non-native plant species, changed populations of native browsers, and fragmentation. Directly or indirectly all of these changes may be related to grazing. Grazing removes forage, which may reduce fuels and thus exclude fire. Roads associated with grazing allotments serve as fire breaks when bisecting grasslands and woodlands and may also interfere with hydrology by redirecting runoff and reducing sheetflow. Also, grazing creates sites for exotic plants to take root (Stoddart et al. 1975).

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[1] Steve Baker (2002) Archeologist, Centuries Research, Inc, Montrose, Colorado. Pers.Comm.
[2] Alan Reed (2002) Archeologist, Alpine Archeology Consultants, Montrose, Colorado. Pers.Comm.
[3] Marie Templeton (2003) Historian, Rimrocker Historical Society of Western Montrose Co., Nucla, CO.

The introduction of livestock to Uncompahgre Plateau rangelands coincides with a period of prolonged drought in the late 1800s. Although the native flora evolved with periodic drought, the added stress of grazing during drought may have shifted the successional trajectory from perennial grass cover to one that favors woody species (Grover & Musick 1990). One potential mechanism for this shift might be that drought reduced the ability of grasses to reproduce sexually, whereas coincident grazing reduced the ability of grasses to reproduce vegetatively (Neilson 2003). The impact of climate vs grazing on vegetation change has been much debated, but the two agents probably acted synergistically.

The ubiquity of grazing in the West has confounded studies of the ecological effects of prolonged drought vs grazing on grasslands and woodlands since it is difficult to find reference areas that have not been grazed. Even where grazing was terminated decades ago we do not know what irreversible changes occurred. Changes probably include altered species compositions, changed soil properties, destruction of protective biotic crusts and erosion. Extensive habitat treatments during the 1930s-1970s to improve forage for livestock or game probably also affected the soil resource adversely. Management treatments continue to employ the use of heavy equipment, though objectives and methods may have changed.

RESEARCH OBJECTIVES

The principal question driving this study was to understand the dynamics and natural disturbance regimes operating in the piñon-juniper zone of the Uncompahgre Plateau at present and prior to the introduction of livestock. One major premise of this research is that no existing model of woodland dynamics adequately addresses all developmental stages of piñon-juniper woodlands. Failure to acknowledge dynamics beyond the canopy closure stage has led to an assumption that most woodlands are "overmature" and outside their historic range of variability. This idea was reinforced by management prescriptions that described only four seral stages. The fourth stage included most landscapes that contain piñon pine or juniper trees, even though this

stage may last longer than the other three stages combined. Furthermore, the presence of dense and presumably young stands near the ecotones has often been interpreted as trees invading other vegetation, and has been attributed to grazing (e.g., Great Basin: Tausch and West 1988, Blackburn and Tueller 1970). However, no studies have compared the rates or timing of increases in these places to dynamic changes that occurred in stable woodlands. No studies consider that cycles of invasion and dieback may be part of the long-term dynamics of piñon-juniper woodlands. If they are, these cycles should be coincident with climate cycles, derivable from tree rings. Furthermore, if invasion cycles exist, the question would change from "is invasion occurring?" to "Is the current rate and extent of invasion outside of the natural range of variability?"

Invasion is thought to be the product of fire exclusion, yet the historic fire return interval has not been determined for Uncompahgre Plateau woodlands. Restoration requires knowledge of the fire regime that occurred prior to the introduction of livestock, and how fire shaped or constrained the ebb and flow of trees into grasslands in the past. This research investigated the preceding data gaps through the following objectives and approaches.

Objective 1: Describe current stand structures and a typical development sequence for piñon-juniper woodlands on the Uncompahgre Plateau

Approach:

1. Determine stand ages of woodlands from different watersheds and topographic positions throughout the study area.

2. Determine characteristics of physical stand structure for stands of different ages.

3. Use a chronosequence of stand structures to infer the typical pre-settlement developmental sequence for piñon-juniper woodlands.

One primary goal of restoration on the Uncompahgre Plateau is "to change the distribution of plant age classes to match a more natural distribution"

(Uncompahgre Plateau Partners 2003). Objective 1 will test assumptions of the vegetation management plan. Specifically, this approach will identify current and historic distribution patterns of piñon-juniper in order to highlight potential priority areas for restoration, based on the departure of age distributions from the historic condition. The temporal baseline for determining departures from the historic condition will be 1881, the year that livestock were first introduced to the Uncompahgre Plateau.

Objective 2: Describe the historic disturbance regime of piñon-juniper woodlands on the Uncompahgre Plateau.

Approach:

1. Use multiple lines of evidence found at each sampling site to infer natural disturbance agents that were historically important.

2. Identify the natural disturbance regime for piñon-juniper. Regime parameters include disturbance type and distribution, spatial extent, frequency, return interval and magnitude.

The piñon-juniper literature focuses on wildfire as the most important disturbance agent acting on woodlands. However, the importance of other types of disturbance has become apparent following drought conditions that began in 1999 and continue to present. Mortality and stress related to the drought conditions are shaping vegetation in significant ways that will continue to constrain ecological functions well into the future. A range of variability study examines the historic record for evidence of the frequency and severity of these agents in the past. Results from this study will allow a more detailed comparison between patterns resulting from natural processes to those created through managed disturbances such as woodcutting, rollerchopping, hydro-axe, and prescribed fire.

Objective 3: Describe changes to stand structure that have occurred following the introduction of livestock to the Uncompahgre Plateau (c. 1880).

Approach:

1. Identify piñon-juniper sites that depart from the reference condition.
2. Describe growth patterns of trees in these sites and compare to growth patterns of trees where stand structure is assumed to be stable.

Piñon-juniper literature often emphasizes that grazing has caused changes in vegetation structure through fire exclusion and subsequent tree invasion. Restoration planning requires knowledge of what these changes were, and whether they are ubiquitous throughout the p-j zone or tend to be restricted to predictable parts of the landscape.

The three overarching objectives were met through a series of four field studies carried out from 2000 to 2003. The four studies share similar objectives and relied on the same general types of data collection and measurements, but differed in their distribution of sampling points. I will refer to them as case studies to underscore these differences when presenting outcomes. Because sampling methods varied among the four studies, they are described below when each case study is introduced. Regardless of sampling methods, sample processing and analysis followed similar protocols, which are described in a general methods subsection that follows the introduction to the four case studies.

STUDY AREA

The majority of data were collected on the Uncompahgre Plateau, but some sites were also sampled east of the Uncompahgre Plateau in the Gunnison Gorge and Black Canyon of the Gunnison National Park (Fig. 2). The Uncompahgre Plateau lies at the

eastern edge of the Colorado Plateau, a broad uplift that contains parts of four western states. The Uncompahgre Plateau is about 200 km long and covers almost 6000 square km (Uncompahgre Plateau Partners 2003). The majority of parent material is derived from sedimentary rocks (National Cooperative Soil Survey 1995). Piñon juniper woodlands are found on all sides of the Uncompahgre Plateau between about 1800-2280 m elevation (6000'-7500', Uncompahgre Plateau Partners 2003). Most of the piñon-juniper cover-type occurs on gently sloping mesas, steeper canyon walls, or colluvium that has collected in the canyons or at the base of slopes.

The nature of woodland communities varies with elevation and soil moisture. Below 1980 m (6500') piñon-juniper occurs with low shrubs such as *Artemesia sp.* or *Ephedra sp.* Precipitation in this zone averages approximately 38 cm/year (15"), though this varies by location and from year to year. Above 1980 m, where annual precipitation may range from 38-48 cm /year (15-19"), piñon-juniper occurs with a taller, mountain shrub community that includes Gambel oak, serviceberry, and mountain mahogany. Sagebrush can also be found in this community. Above 2280 m piñon-juniper grades into a mountain shrub community where piñon pine becomes increasingly rare and may be replaced by aspen or ponderosa pine.

On the Gunnison Gorge uplands, woodlands occur at slightly higher elevations than are found on the Uncompahgre Plateau, and give way to oak brush at the highest elevations. The Gunnison Gorge doesn't reach a high enough elevation for other kinds of forests to form, though occasional ponderosa pine trees occur. Douglas fir trees grow on the steep, rocky cliffs of the inner gorge.

There are no climate stations in piñon-juniper woodlands, but nearby stations with long records are located in Grand Junction, Delta, Montrose, and Norwood (Table 2 and Fig. 2, 3). Note that though temperature and precipitation amounts vary among stations, seasonal distribution patterns are strikingly similar. June is nearly always very dry. Maximum precipitation generally occurs in August following the mid-summer drought, but a second peak of precipitation occurs in spring. In the summer, precipitation comes from orographic uplift and convectional storms and is patchy from one location to another (National Cooperative Soil Survey 1995). Over long periods of time, predictable patterns of precipitation can be described based on landscape
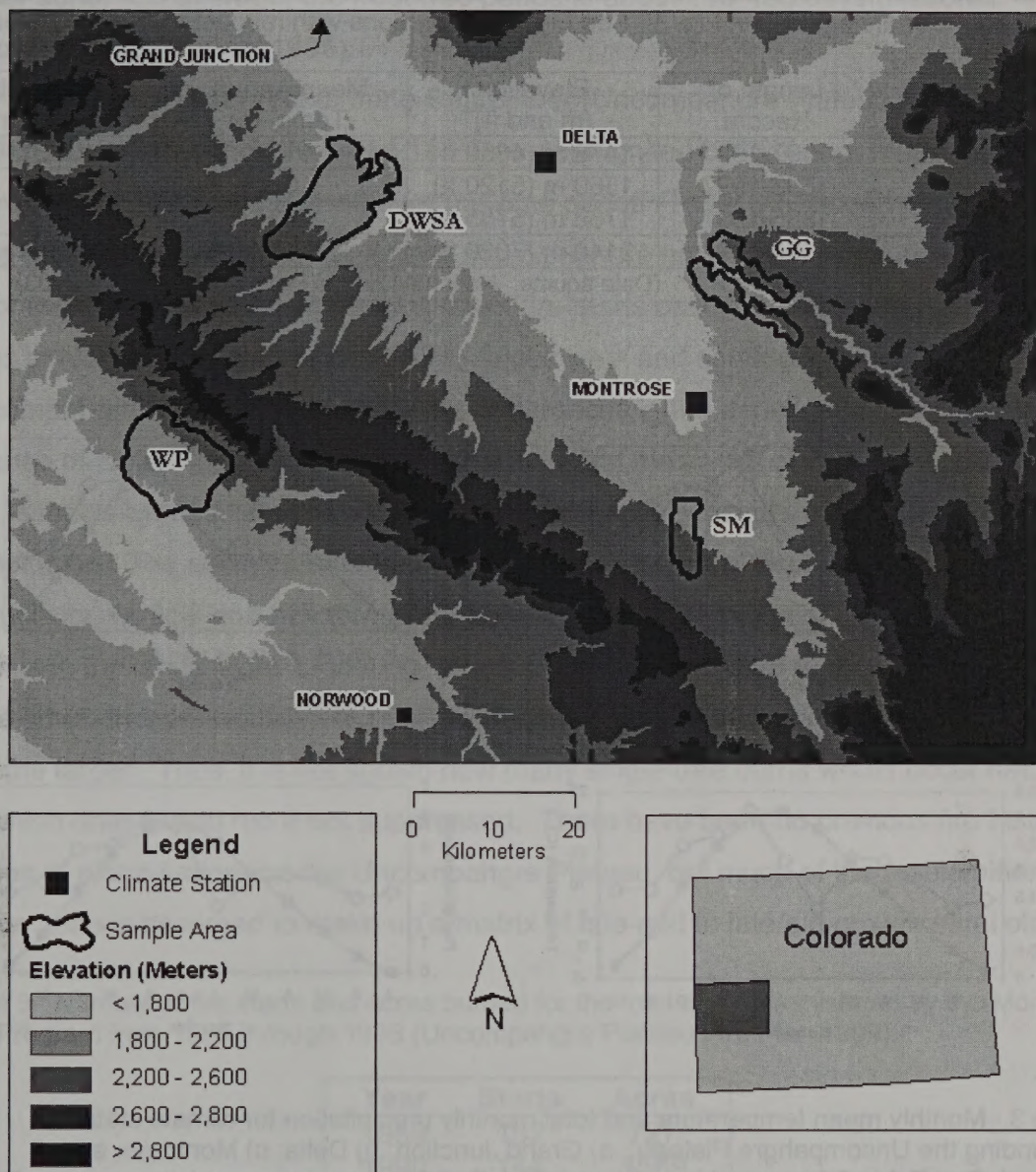
Figure 2. Location of sampling units within the Uncompahgre Plateau study area. DWSA is the Dominguez Wilderness Study Area located north of Escalante Forks and west of the city of Delta; GG is the Gunnison Gorge Wilderness Area and the Black Canyon of the Gunnison National Park; SM is the Sims Mesa and upper Government Springs area, located south of the city of Montrose; and WP is the Windy Point area surrounding Campbell Creek and the upper Atkinson Mesa Area, located west of the town of Nucla (not shown). Location of climate stations with long instrumental records are indicated.

Table 2. Elevation, mean annual temperature and total annual precipitation for Uncompahgre Plateau area climate stations in Fig. 3. See Fig. 2 for locations with respect to sampled areas.

	Length of Record	Elevation (m and ft)	Mean Annual Temp. (c)	Mean Total Precip (cm)
Grand Junction	1899-1997	1478 m (4850 ft)	11.5	22.1
Delta	1893-1997	1560 m (5120 ft)	10.2	19.7
Montrose	1885-1997	1763 m (5785 ft)	9.3	24.3
Norwood	1930-1997	2140 m (7020 ft)	7.1	39.1

(Data source: National Climate Data Center, NOAA 2003)
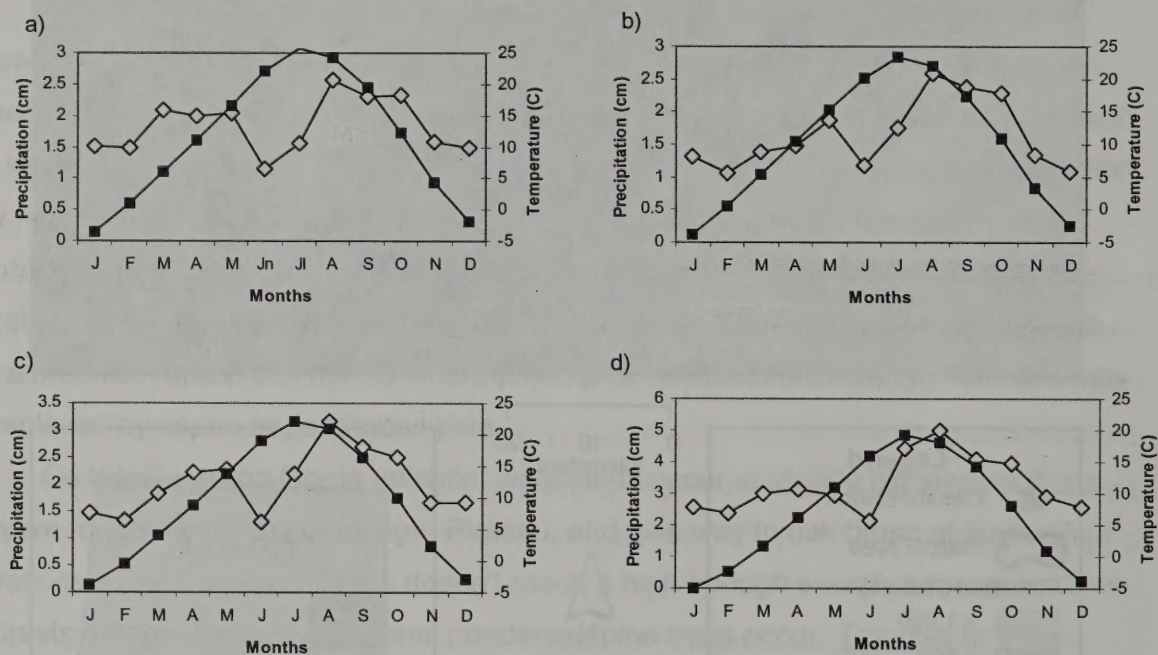
Figure 3. Monthly mean temperature and total monthly precipitation for climate stations surrounding the Uncompahgre Plateau. a) Grand Junction; b) Delta; c) Montrose; and d) Norwood. See Table 2 for record lengths and elevations. ◊ precipitation, ■ temperature. Data from National Climate Data Center: http://cdo.ncdc.noaa.gov/pls/plclimprod.

influences on weather patterns. For example, the Dominguez Wilderness Study Area (DWSA, Fig. 2) lies east of the crest of the Uncompahgre Plateau in a rainshadow, whereas more precipitation falls in the piñon-juniper zone of Sims Mesa (SM, Fig. 2) than falls in DWSA or WP (WP, Fig. 2) at similar elevations. The length of the growing season varies with elevation, but typically lasts from May until September in the piñon-

juniper zone. On average, the frost-free period is about 110-150 days (National Cooperative Soil Survey 1995).

Wildfires typically occur June-September (Uncompahgre Plateau Fire Plan 1999). From 1988-1998, 79% of 1,189 fires were ignited by lightning, and accounted for 75% of the 21,722 acres burned over this time period (Table 3). Though natural fire starts are common in the piñon-juniper zone, they are not evenly distributed across the Uncompahgre Plateau. A higher density of fire-starts occurs on ridges surrounding the towns of Nucla and Naturita, and on hill slopes west and south of Montrose (Uncompahgre Plateau fire Plan 1999). Differences in the density of fire starts occur because of topographical differences, which control the tracks of convective storms. Also, especially in early to mid-summer, electrical activity occurs without significant precipitation. The ability to burn is under topographic control because of changes in productivity, vertical and horizontal fuel connectivity, and ignition sources in relation to position in the landscape. Lightning- struck trees are encountered moderately often, but these small fires are usually suppressed because of the difficulty of control once if they become larger. Thus, it is not known how many single-tree burns would occur naturally vs. which ones would run if not suppressed. There have been no previous fire history studies of piñon-juniper on the Uncompahgre Plateau, but much of the stable piñon-juniper zone is assumed to make up a matrix of late-mid to late/old growth seral stages

Table 3. Number of fire starts and acres burned for the total area administered by the Montrose Fire Program from 1989 through 1998 (Uncompahgre Plateau Fire Plan 1999).

Year	Starts	Acres
1989	152	727
1990	144	1589
1991	96	82
1992	82	16
1993	108	293
1994	298	12,633
1995	121	668
1996	206	1,818
1997	86	88
1998	100	1,808
Total	1189	21,722

that historically supported infrequent, hot crown fires that were limited in extent due to topographic fire breaks (Uncompahgre Plateau Fire Plan 1999). In contradiction, management prescriptions for these areas call for developing "a landscape pattern that will be largely sustained by naturally occurring, low intensity fire that burns like it used to" (Uncompahgre Plateau Fire Plan 1999). Thus, while resource managers recognize that infrequent, high-intensity fires naturally occurred, fire prescriptions are based on a different set of expectations, probably derived from piñon-juniper fire history studies in other places.

METHODS - Case Studies

Case Study 1: Dominguez Wilderness Study Area (DWSA)
Tasks:
1. Develop methods for sampling piñon pine using an area with limited human influence and low road density.
2. Collect samples for chronology; compare cross-dating between north and south aspects.

The initial pilot area sampled in 2000 is located above Escalante Forks in the Dominguez Wilderness Study Area, west of the city of Delta (Fig. 4). This landscape comprises gently sloping tablelands that rise in elevation from the northeast to the southwest, with deeply incised drainages dissecting the landscape into linear mesa tops and steep-sided draws. Initially, twenty stands were sampled. Later, in 2002, an additional 3 stands were added on flat sites (sites DWSA-F1, F2, & F3).

The initial twenty stands were sampled using 30 meter x 30 meter plots. Ten plots were located on north aspects and ten were located on south aspects between 5 and 30 degrees slope. Only north and south aspects were sampled in order to maximize the amount of variation encountered in stand structures. A complete census of all trees in the plots was used to characterize the age- and size-distributions present

Figure 4. Dominguez Wilderness Study Area (DWSA) sampling unit. See Fig. 2 for location with respect to other sampling units. Sampling area polygon defines woodland extent between Little Dominguez Creek on northwest and Escalante Creek on southeast side using vegetation information from the Natural Diversity Inventory Source (CDOW 2003) and elevation.

in each plot. Each tree taller than 2 meters was mapped and all trees were cored at approximately 10 cm above the ground. Species and diameter at the root collar (DRC) were recorded. Logs and dead standing trees were recorded by species, but no other data was collected. A varying number of seedlings were collected from each plot in order to provide estimates of ages to coring height for sampled trees. Though collected, juniper cores were not aged because of difficulties with cross-dating. The 3 plots on flat sites were sampled using methods described in Case Study 2.

Case Study 2: *Gunnison Gorge & Black Canyon of the Gunnison National Park* *(GG)*
Tasks:
1. Sample age and size structures and amount of coarse woody debris.
2. Collect evidence of past fires when encountered.

In 2001, twenty stands were sampled in the Gunnison Gorge area (Fig. 5). Nine stands were from the north outer rim and eleven stands were from the south outer rim of the Black Canyon. Data was collected along transects using the point-centered quarter method (Barbour et al 1987). Transects were used in order to sub-sample structural variation over a longer distance than could be collected from a fixed-size plot, and to overcome the patchiness of woodlands that may possibly confound data collected from within the smaller plots. Point centers were separated by 25-30 meters. All transects had at least 12 point-centers. If a stand was not large enough to accommodate a full transect, the line was broken into segments that were at least 30 meters apart to avoid overlap of search areas. Two piñon pine cores were collected from each point center along the transect, but no cores were collected from juniper trees. Most cores were
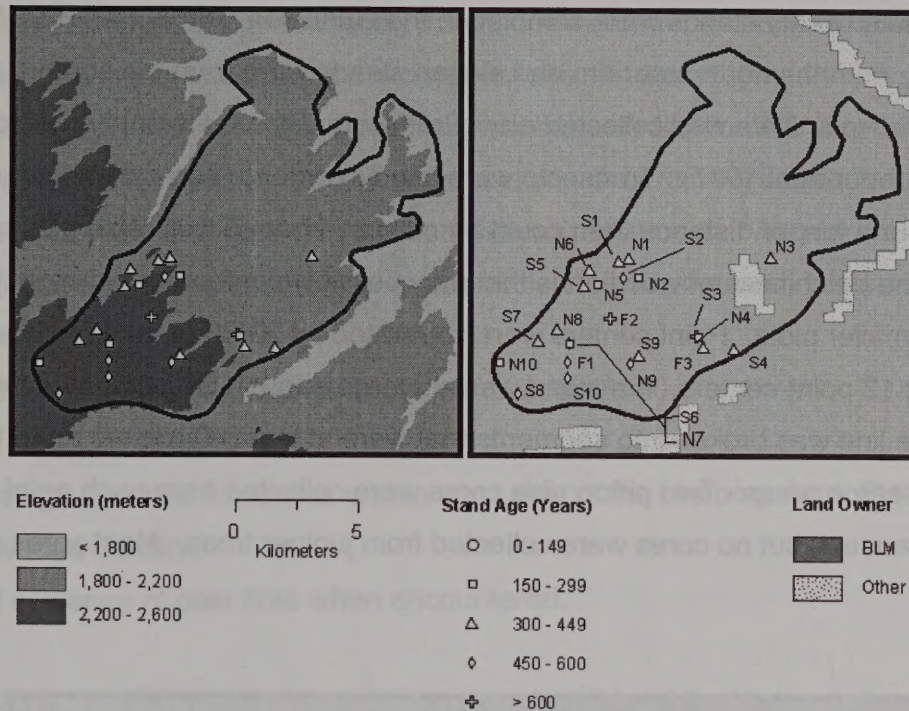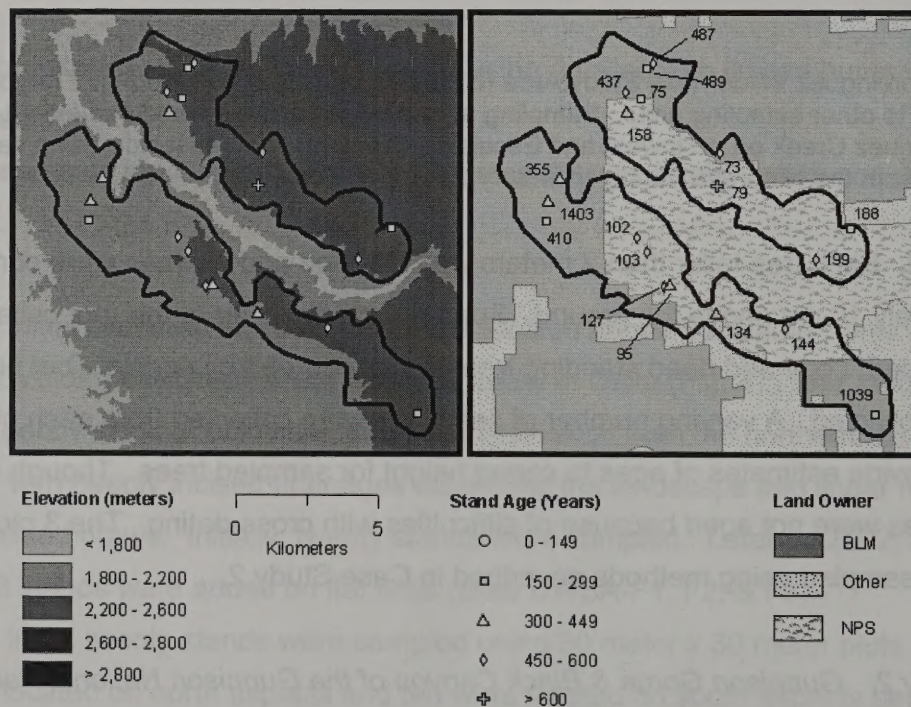

Figure 5. Gunnison Gorge (GG) sampling unit. See Fig. 2 for location with respect to other sampling units. Sampling area polygon is defined by vegetation information from the Natural Diversity Inventory Source (CDOW 2003) and elevation. Polygons do not include steep rock-faces of the inner gorge.

collected from a height of approximately 10 cm. A minimum of 12 point centers provided 24 piñon pine cores for age reconstructions. However, fewer piñon pine cores were collected from sites where this species was sparsely distributed. In addition to collecting cores from live trees, partial cross-sections or cores were collected from the base of dead pine trees whenever the wood was sound enough. Wood from dead trees was only collected from within the 5 m-radius circle surrounding each point center.

Case Study 3: Windy Point and Atkinson Mesa areas (WP)
Tasks:
1. Sample age and size structures on the west side of the Uncompahgre Plateau in an area of low road density.
2. Collect evidence of past fires when encountered.

In 2002, 19 stands were sampled on the west side of the Uncompahgre Plateau (WP), northwest of the town of Nucla (Fig. 6). This landscape has a steeper elevation gradient than DWSA, but is still made up of gently sloping mesas incised by linear drainages. The elevation rises from southwest to northeast, with most sampling sites located on south to southwest aspects.

Stands were sampled along transects using methods identical to case study 2 (GG), except that most sites included twenty point-centers. Two piñon cores were collected from each point center along transects, but no juniper samples were collected. Most cores were collected from a height of approximately 10 cm. Cross-sections were collected from dead piñon pine trees when possible, and basal discs were collected from seedlings and saplings of both species. Cross sections from dead piñon pine trees have not yet been aged.

Elevation (meters)

	< 1,800
	1,800 - 2,200
	2,200 - 2,600
	2,600 - 2,800
	> 2,800

Stand Age (Years)

O	0 - 149
□	150 - 299
△	300 - 449
◇	450 - 600
✛	> 600

Land Owner

	BLM
	Other
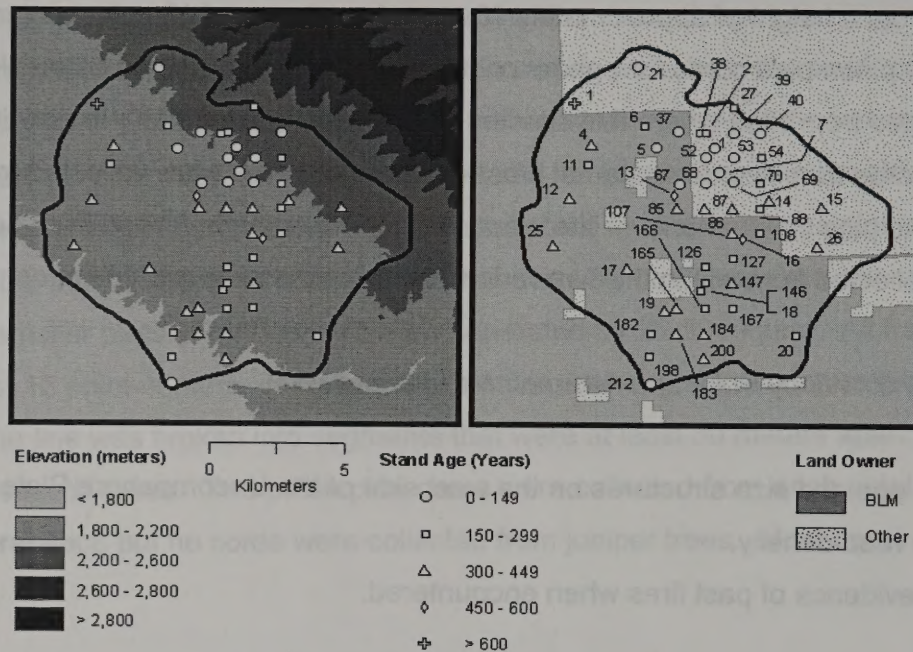
Figure 6. Windy Point and Atkinson Mesa (WP) sampling unit. See Fig. 2 for location with respect to other sampling units. 19 stands were sampled in 2002 (case study 3), and an additional 32 plots were sampled in 2003 (case study 2003). Sampling area polygon is defined by vegetation information from the Natural Diversity Inventory Source (CDOW 2003) and elevation.

Case Study 4: Sims Mesa & upper Government Springs (SM); Campbell Creek in WP area

Tasks:

1. Systematically sample woodland structures along an elevation gradient (Note: Sims Mesa: ecotones not sampled because they occur on private land).

2. Characterize invasion of piñon and/or juniper trees into sagebrush on Sims Mesa.

3. Record mistletoe loads and degree of piñon die-off in all plots.

In 2003, 75 circular plots were sampled from two separate sampling arrays. An array of small, circular plots was used to capture the full range of structural variation found across sampling areas. One array was located west of Nucla near Campbell Creek, and overlapped with sites sampled in 2002 (Fig. 6, 32 plots). The other was

located on Sims Mesa and Government Springs (Fig. 7). Each plot was 314 m² (.03 ha). Plots were separated by approximately 1 km spacing at WP and the southern ¾ of SM. In the northern ¼ of SM, plots were separated by 0.5 km to capture the pattern of tree invasion into sagebrush. In both sampling areas the arrays were aligned along the elevation gradient, but in the SM area sampling was constrained at the highest and lowest elevations by property boundaries between public and private lands. In the WP area private inholdings were excluded from sampling, but private land was not situated on the upper and lower ecotones.

All live and dead trees, saplings and seedlings were recorded by species. Tree diameters were measured for all trees > 4 cm diameter at the root collar (DRC). Smaller trees were mapped but not measured. In addition, total soil depth was measured using a long-handled soil auger. The depth limitation of the tool was 1.75
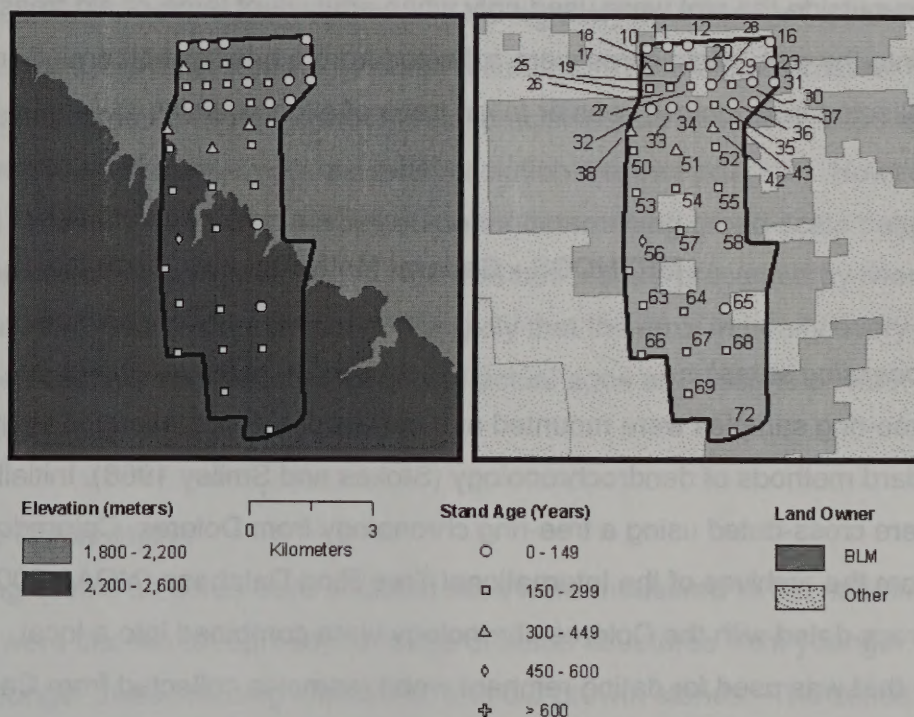
Figure 7. Sims Mesa and upper Government Springs (SM) sampling unit. See Fig. 2 for location with respect to other sampling units. Sampling area polygon is defined by Happy Canyon on the west, Dolores Creek on the northeast and elevation. Sampling area was constrained by boundaries between public and private land. Extensive treatments on Government Springs (southern half of sampling area) are not shown.

meters, and was only exceeded in 4 of 75 plots.

Each site and its surrounding area were searched for evidence of stand disturbance. Each live tree was searched for mistletoe and rated according to the Hawkesworth scale (Hawkesworth 1977). Dead trees were classified into decay categories by qualitatively scoring the degree of decay (0-2) for needles, twigs, branches, bark, and structural support (propped up by branches vs collapsed vs very deteriorated). Dead trees were assumed to be recently dead (last 5 years) if twigs and branches were present in lifelike amounts, bark was mostly intact, and tree was standing or supported above the ground by branches if fallen. Notes were made if visual evidence of bark beetles were present; otherwise cause of death was recorded as unknown. Notes were made for each tree killed by woodcutting. Up to six piñon pine trees from inside the plot or nearby were cored to provide estimates of stand ages for dominant size cohorts and to develop age-diameter relationships for unsampled trees. Trees outside the plot were used only when equivalent large or old trees were not rooted into the plot. Most cores were collected from a height of 10 cm. Samples were not collected from juniper trees or fallen trees of either species.

METHODS - General Methods

3.2.3.2 Processing samples

All tree-ring samples were mounted and surfaced in preparation for analysis using standard methods of dendrochronology (Stokes and Smiley 1968). Initially samples were cross-dated using a tree-ring chronology from Dolores, Colorado obtained from the archives of the International Tree Ring Database (NOAA 2000). Samples cross-dated with the Dolores chronology were combined into a local chronology that was used for dating remnant wood (samples collected from Case Study 3 (GG) only). In general, only mortality dates for trees from decay classes I and II (Table 3.2) could be estimated because higher decay classes showed significant erosion or deterioration of outer rings or sapwood.

Tree ages were determined from the number of growth rings on cross-dated cores. Age adjustments were made for samples that missed the tree pith by first estimating the distance between the inner-most tree ring and the pith using a template of concentric circles, and second by multiplying this distance by an empirically-determined factor based on the average number of rings per mm for complete cores (2.53 x mm from pith). This method was employed because the initial growth of piñon pine seedlings is very slow, with several to many rings per mm within the first 5 to 10 mm from the pith. An additional correction factor was added to the core age to correct for the time needed for each sampled tree to reach the coring height. The age-to-coring-height correction was determined empirically from regression of seedling age on seedling height (0.9118 x height in cm). Piñon trees that grow in the open show rapid growth after a short period of suppression, but the majority of trees had slow, or very slow, initial growth.

Because of pronounced suppression during early development, establishment dates for most samples are probably underestimated. Therefore, estimated establishment dates do not represent annual precision, and cannot be used to pinpoint discrete events. For many trees, decadal resolution was not possible. However, estimated establishment dates are adequate for determining broad-scale patterns for piñon pine across the sampling units. Age distributions are presented by twenty-year age classes to reflect this uncertainty. It is likely that the error in nearly every case goes only in one direction, and that the majority of actual ages are close to or older than what has been reported

Tree-Ring Chronologies

Ring-widths on cores from selected sites were measured to the nearest .001 mm. The sites were chosen to represent a range of stand structures from younger, post-fire stands, younger trees invading shrubland, and old-growth stands. The series of ring-width measurements from each tree was standardized by its mean ring-width in order to preserve the long-term growth trend of each tree. Standardized tree-ring series were averaged together into site chronologies. The resultant site chronologies are displayed as time-series graphs that show the inter-annual pattern of wide and narrow rings for

each site, yet also indicate longer periods of slow or rapid growth. The pattern of growth just prior to and during chronic grazing can be compared among young and old stands to determine the timing and nature of growth patterns that diverge.

Stand Age Estimates – All Case Studies

All stand ages are based on samples collected from piñon pine trees. Though juniper trees might be older in some stands, their ages were not sampled and could not be used to derive stand ages. This probably introduces significant error for some stands, particularly where juniper dominates stand densities. In lieu of juniper ages, the shape of the diameter distributions of juniper trees in each stand was recorded for comparison among stands. The juniper size-distribution tended to conform to a relatively small number of shapes. The most frequent were: bell-shaped, dominant in the larger size classes, some in all size classes, few in all size classes, or no juniper trees.

After all data for each stand was gathered, stand ages were estimated based on several lines of evidence. The primary evidence was the age distribution of living trees from each stand. This data was inspected in both age-frequency plots and diameter-age scatterplots. Most stands had one to several trees that were significantly older than the majority of trees. Where significant time has passed since stand initiation or a major disturbance event it is not possible to distinguish whether these old trees were relicts from a previous stand or were remnants of an early cohort in the current stand. In most cases age estimates do not include these outliers if old trees were not distributed throughout the stand or if the correction factors added for missed piths and coring heights were large. To be conservative, where a gap exists between the majority of tree ages and the oldest trees, stand age estimates are taken as the point in time when at least 2-3 trees are present. Other contributing lines of evidence were based on diameter distributions of both tree species and the distribution of sizes and states of decay of dead trees.

Evidence of Fire

All sites were carefully searched for evidence of fire. No identifiable fire scars were found on any trees in sampled sites. However, lightning struck trees with charcoal were sometimes encountered, and occasionally were found in sample sites. Evidence of previous stand-replacing fires was frequently encountered. The most compelling evidence for a previous stand-replacing fire was charred wood or charred snags scattered throughout a stand. Sometimes it was evident that logs had been burned, but the charcoal was eroded away. Other stand features also contributed to perceptions that stand-replacing fire had occurred in the past, but were not considered conclusive without some evidence of charcoal in most cases. Contributing evidence was the presence of larger, obviously open-grown trees surrounded by a closed canopy of straight-stemmed trees (generally not less than 10 cm diameter at the root collar), or a site where the bigger trees were evenly-distributed and of similar sizes (Fig. 8). Straight, single stems and lack of lower branches suggest that the stand was originally dense but is self-thinning. When these stand structures were encountered a wider search was made for charred wood if none was encountered within the plot. However, a stand was labeled post-fire only if charcoal was eventually found. Charcoal was very difficult to find in stands older than 250 years, but did occur up to about 500 years in some cases.

Figure 8. Example of piñon-juniper woodland with evenly-spaced trees and similar-sized diameters. Note lack of coarse woody debris on woodland floor. Often removing litter from the base of the tree would expose wood fragments from nurse logs, usually too decayed to have charcoal.

Observation of contemporary fire suggests that nearly all trees within the fire perimeter are killed, even if the fire extent is small. Most logs and snags present prior to the fire are consumed by the fire. Thus, abundant woody debris suggests that a fire has not occurred for some time, though it is possible that fire caused the death of these logs. Where charred logs are present in the stand, the mortality date could be determined to within a few years of the actual date by cross-dating with another chronology if outer rings are still intact (Villalba and Veblen 1998). However, after about 50 years (or less) there is significant erosion of outer tree-rings, and after more than 100 years (or less) there is a substantial deterioration of sapwood (personal observation). Loss of outer rings precludes estimating a fire date. Minimum time since fire can be estimated based on the ages of the oldest living trees in a stand. However, post-fire establishment of trees can lag behind fire occurrence by decades or more, so establishment dates of the initial trees probably underestimates the fire date.

In old stands where charcoal has weathered off of woody debris there might be nothing left to indicate that woodlands generated following stand-replacing fire. Also, smaller logs probably decay more quickly than larger logs, and piñon pine wood decays more quickly than juniper wood. This means that if centuries have passed since the last fire, the debris most likely to persist is from large-diameter trees, especially juniper species. Observation of logs in recent burns shows that char tends to be more prominent on older piñon pine and juniper logs where wood surfaces were exposed prior to the fire. Younger trees are often killed with no evidence of char. Thus, lack of charcoal in stands does not mean a stand has not regenerated following fire. It merely means that fire cannot be identified as the primary agent of stand renewal.

RESULTS

Stand structure and development

Tabulated stand summaries show stand ages ranging from 40 to more than 700 years (Fig. 9, Table 4, Figs. 4-7). Peak stand age is 200-250 years (N = 21 of 136), but stand ages are distributed over the entire age range, with only 5 stands older than 550
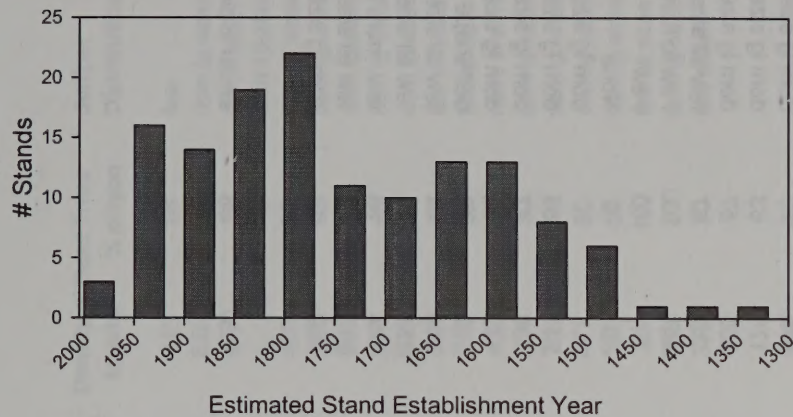
Figure 9. Distribution of 138 estimated piñon-juniper stand ages for stands sampled from 2000 to 2004 in the Uncompahgre Plateau area.

years. The final column in Table 4 describes the shape of the juniper size-distribution for each stand. Where large juniper trees dominate the basal area, stand ages are most likely underestimated. Estimates of stand age were determined from piñon pine trees only, and are conservative in that the oldest tree on some sites may be older than what has been reported as the stand age. One example of a juniper-dominated stand that may be older than the estimated age is GG-102 (Fig.10). The age estimate for GG-102 is 550 years (Table 4), but the stand has a number of juniper trees that are much larger than the oldest piñon pine trees, and also larger than most dead trees (Fig. 10a,b).

Of the 33 stands where juniper dominates the large size classes, 15 fall into the 200- to 300-year range of ages. This might mean that the peak of stand ages 200-250 years ago (Fig. 9) is an artifact of not aging juniper trees and that these stands are older than what has been reported. However, many other stands also show an increase in the density of trees beginning 200-300 years ago. Tree density in all sampling areas appears to increase beginning in the early to mid-1700s (Fig. 11), long before the introduction of livestock. The rapid increase in the number of trees across sampling areas beginning in the 1700s could be due to higher rates of establishment and survival,

Table 4. Stand summaries for all sites in four Case Studies from the Uncompahgre Plateau area. See Fig. 2 for sample area locations.

Site	Elev (m)	Aspect	Slope (°)	Stand Age[1]	Fire[2]	Density of Live Trees trees/ha	% pinyon	Total Basal Area BA(m^2)/ha	% pinyon	Density of Dead Trees logs/ha[3]	% pinyon	Juniper Distribution[4]
Case Study 1												
DWSA-F1	2367	E	3	540	1	485	71	44	70	490	82	P dom. lg class
DWSA-F2	2277	E	5	520	1	652	71	48	62	728	91	few all sizes
DWSA-F3	2196	NE	3	420	1	525	69	38	41	679	74	dom lg sizes
DWSA-N1	2159	N	14	400	1	1167	78	57	32	.	.	dom lg sizes
DWSA-N2	2186	NW	16	240	1	811	71	38	39	122	73	dom lg sizes
DWSA-N3	1984	SE	10	340	0	956	72	44	44	356	56	few all sizes
DWSA-N4	2130	N	19	220	0	956	66	41	37	178	75	dom lg sizes
DWSA-N5	2152	NW	20	250	1	989	65	41	34	178	63	dom lg sizes
DWSA-N6	2158	NW	22	375	1	1078	74	68	29	256	57	dom lg sizes
DWSA-N7	2328	N	24	290	1	767	81	32	82	33	67	few all sizes
DWSA-N8	2314	NE	20	440	1	467	95	20	97	89	100	Few to none
DWSA-N9	2221	N	20	450	0	622	89	30	94	67	50	Few
DWSA-N10	2419	NW	12	200	1	356	100	31	100	0	0	None
DWSA-S1	2169	S	22	400	1	356	47	31	24	.	.	dom lg sizes
DWSA-S2	2177	S	23	500	1	522	43	66	13	211	63	dom lg sizes
DWSA-S3	2130	S	30	650	0	378	56	63	35	133	42	dom lg sizes
DWSA-S4	2125	S	23	340	1	433	49	31	23	133	50	dom lg sizes
DWSA-S5	2215	SE	7	350	1	1189	28	67	17	222	10	bell shape
DWSA-S6	2328	S	15	400	1	1056	78	45	31	200	44	few all sizes
DWSA-S7	2376	SE	25	420	1	478	58	42	30	256	61	few all sizes
DWSA-S8	2422	SW	20	520	1	667	67	44	41	144	38	few, more in lg
DWSA-S9	2206	S	22	440	0	578	73	39	47	211	58	few all sizes
DWSA-S10	2308	SW	18	500	0	467	69	44	40	100	44	dom lg sizes
Case Study 2												
WP-1a	2116	SW	5	600	0	1035	68	58	60	1057	86	similar to pinyon

Table 4 continued.

Site	Elev (m)	Aspect	Slope (°)	Stand Age[1]	Fire[2]	Density of Live Trees trees/ha	Density of Live Trees % pinyon	Total Basal Area BA(m²)/ha	Total Basal Area % pinyon	Density of Dead Trees logs/ha[3]	Density of Dead Trees % pinyon	Juniper Distribution[4]
WP-2	2216	S	9	200	1	1175	73	45	54	246	66	few
WP-4	2056	S	6	380	1	624	59	39	39	828	85	dom lg sizes
WP-5	2096	SW	5	120	1	351	31	16	15	547	51	few, mainly dom 10-20cm
WP-6	2141	W	8	160	1	519	55	25	21	469	22	dom lg sizes
WP-7	2166	S	9	140	1	535	63	20	33	567	43	dom lg sizes
WP-11	2016	W	4	260	1	918	64	45	23	828	75	dom lg sizes
WP-12	1931	SW	4	300	0	725	46	50	18	847	46	dom lg sizes
WP-13	2081	S	6	480	0	884	65	36	33	643	73	dom lg sizes
WP-14	2191	S	11	400	1	850	74	36	51	688	90	few all sizes
WP-15	2307	SE	25	420	1	1140	84	64	56	216	82	few all sizes
WP-16	2081	SE	7	480	1	755	66	31	42	407	80	more in sm sizes
WP-17	1875	W	7	380	0	611	24	49	6	554	30	dom lg sizes
WP-18	1941	S	5	240	1	674	47	30	16	796	48	dom lg sizes
WP-19	1850	SW	9	320	0	638	45	49	14	471	60	dom lg sizes
WP-20	1986	S	3	240	0	513	43	36	11	567	55	dom lg sizes
WP-21	2262	SW	11	100	0	658	86	22	78	57	100	few all sizes
WP-25	1850	SW	8	300	0	627	36	51	11	382	33	dom lg sizes
WP-26	2146	S	14	420	1	516	46	46	16	376	70	bell shape
Case Study 3												
GG-73	2559	SE	20	550	0	482	58	64	53	309	65	similar to pinyon
GG-75	2461	W	5	150	0	175	95	4	94	0	0	few
GG-79	2349	NW, E	5	700	0	262	65	39	61	276	81	some all lg sizes
GG-95	2224	SW	27	350	0	187	33	33	8	164	61	dom lg sizes
GG-102	2120	W	19	500	0	337	59	36	19	411	64	dom lg sizes
GG-103	2149	W, NW	15	500	0	524	63	58	32	607	71	few all sizes
GG-127	2221	W, NW	14	450	1	124	42	17	15	369	50	dom lg sizes

Table 4 continued.

Site	Elev (m)	Aspect	Slope (°)	Stand Age[1]	Fire[2]	Density of Live Trees		Total Basal Area		Density of Dead Trees		Juniper Distribution[4]
						trees/ha	% pinyon	BA(m²)/ha	% pinyon	logs/ha[3]	% pinyon	
GG-134	2202	W	33	400	0	233	21	45	3	246	44	dom lg sizes
GG-144	2461	W	23	550	0	253	66	34	52	233	50	sim to p for >20cm
GG-158	2350	SW, W	28	350	0	215	47	45	5	276	84	dom lg sizes
GG-188	2587	SE, S	27	200	1	370	73	33	41	456	74	dom lg sizes
GG-199	2448	SE, SW	7	500	1	278	48	41	34	78	88	some in all sizes
GG-355	1967	E	15	300	1	391	11	34	4	297	0	bell shape
GG-410	2124	W	9	250	0	717	13	76	2	223	45	dom lg sizes
GG-437	2380	NW	6	500	1	521	77	51	76	244	82	few all sizes
GG-487	2360	S, NW	4	450	1	325	52	32	51	284	54	similar to pinyon
GG-489	2295	SW, S	24	250	1	260	41	49	9	441	56	dom lg sizes
GG-1039	2376	SW	10	250	1	1514	95	53	76	255	62	few
GG-1403	2107	SW, W	11	350	0	491	25	46	2	241	50	bell shape
Case Study 4												
WP-1b	2206	W	3	120	0	32	0	0	0	923	100	few small sizes
WP-27	2395	WSW	23	250	0	318	100	17	100	64	100	none
WP-37	2168	SSE	5	90	0	477	73	8	24	0	0	few
WP-38	2225	WSW	10	265	0	828	65	21	58	318	100	bell shape
WP-39	2285	W	5	90	0	159	100	3	100	0	0	none
WP-40	2261	S	17	40	1	32	100	0	100	95	100	none
WP-52	2226	W	6	115	1	318	100	2	100	64	0	none
WP-53	2199	SW	7	140	0	1401	82	30	72	286	56	few
WP-54	2273	WSW	2	270	0	637	85	44	83	64	100	few
WP-67	2104	WNW	6	120	1	350	82	9	71	796	64	few
WP-68	2119	SE	4	90	1	859	56	11	69	573	89	most small
WP-69	2150	S	19	90	1	477	60	13	76	605	26	sm sizes only
WP-70	2153	NE	8	165	1	541	94	20	84	64	0	few sm sizes
WP-85	2041	SW	2	400	0	732	52	38	19	605	53	bell shape

Table 4 continued.

Site	Elev (m)	Aspect	Slope (°)	Stand Age[1]	Fire[2]	Density of Live Trees		Total Basal Area		Density of Dead Trees		Juniper
						trees/ha	% pinyon	BA(m^2)/ha	% pinyon	logs/ha[3]	% pinyon	Distribution[4]
WP-86	2060	NW	12	400	0	764	67	31	43	955	77	some all sizes
WP-87	2072	SE	8	430	1	1019	84	26	65	382	75	few sm sizes
WP-88	2148	S	16	230	0	1082	56	58	15	668	81	dom lg sizes
WP-107	2050	N	7	440	0	1050	79	26	52	382	75	bell shape
WP-108	2108	W	5	240	0	1082	71	53	18	1082	71	bell shape
WP-126	1980	NW	8	250	1	1910	73	32	46	732	61	bell shape
WP-127	2035	SW	4	290	1	764	67	24	34	382	92	most small
WP-146	1966	NNW	9	225	1	987	84	20	53	923	72	few all sizes
WP-147	1884	SE	13	375	1	891	61	48	36	414	31	bell shape
WP-165	1860	NW	3	325	0	605	53	40	22	637	45	dom lg sizes
WP-166	1872	ESE	9	150	0	637	5	68	1	255	25	bell shape
WP-167	1919	SE	9	175	0	382	8	22	3	255	63	some all sizes
WP-182	1793	S	9	270	0	541	12	51	5	700	18	bell shape
WP-183	1845	W	6	400	0	796	24	51	12	477	13	bell shape
WP-184	1838	W	6	400	0	376	41	36	18	553	48	some all sizes
WP-198	1766	W	2	230	1	133	0	20	0	508	26	few all sizes
WP-200	1807	W	3	410	0	464	33	39	6	575	38	some all sizes
WP-212	1729	WSW	20	90	0	306	20	51	2	61	0	few lgr sizes
SM-11	2063	E	6	65	0	191	67	3	88	64	100	sm sizes only
SM-17	2108	NE	5	300	0	414	23	40	14	159	60	bell shape
SM-19	2080	ENE	2	270	0	637	30	35	19	573	28	bell shape
SM-23	2026	N	5	75	0	382	100	2	100	32	100	few to none
SM-32	2161	N	5	125	0	764	42	39	11	446	57	bell shape
SM-33	2141	N	2	110	0	796	92	14	62	32	100	few to none
SM-35	2096	E	3	150	0	286	100	3	100	127	50	few to none
SM-37	2080	S	5	75	0	64	100	0	100	0	0	few to none
SM-50	2197	N	1	150	0	923	69	24	41	318	40	few all sizes

Table 4 continued.

Site	Elev (m)	Aspect	Slope (°)	Stand Age[1]	Fire[2]	Density of Live Trees trees/ha	% pinyon	Total Basal Area BA(m[2])/ha	% pinyon	Density of Dead Trees logs/ha[3]	% pinyon	Juniper Distribution[4]
SM-51	2189	NNW	6	325	1	732	52	41	21	541	76	few all sizes
SM-52	2130	N	2	200	0	764	33	19	23	509	94	sim to P
SM-53	2234	W	8	245	1	1114	77	34	38	414	69	few all sizes
SM-54	2204	NNE	2	210	1	859	56	33	16	541	59	bell shape
SM-55	2166	NNE	2	230	0	414	38	32	27	191	17	dom lg sizes
SM-56	2295	N	5	550	0	605	68	56	58	223	57	few all sizes
SM-57	2238	N	2	170	0	1432	87	37	41	286	78	few all sizes
SM-58	2204	NNE	3	110	0	1019	97	12	99	0	0	few to none
SM-60	2299	N	4	200	1	732	78	32	61	286	44	few all sizes
SM-63	2348	N	3	215	1	318	90	25	98	223	86	few to none
SM-64	2327	ENE	3	185	1	509	100	14	100	159	40	none
SM-65	2288	N	2	150	1	987	94	24	94	0	0	few to none
SM-66	2392	E	4	180	1	442	80	37	83	243	55	few all sizes
SM-67	2355	NNE	3	200	1	987	97	27	99	127	100	few to none
SM-68	2328	N	4	185	1	1019	84	33	95	286	67	few sm sizes
SM-69	2387	SE	4	160	1	923	97	30	92	32	100	few to none
SM-72	2383	ENE	2	180	1	923	97	34	93	64	100	few to none
SM-10*	2078	SW	12	75	0	350	91	6	63	0	0	few to none
SM-12*	2056	WNW	4	0	0	0	0	0	0	0	0	none
SM-16*	2025	NNE	3	60	0	0	0	0	0	64	100	none
SM-18*	2085	NW	8	250	0	923	34	29	11	477	73	reverseJ
SM-20*	2058	ENE	4	70	0	446	79	3	78	0	0	sm sizes only
SM-25*	2119	SSE	4	200	0	477	13	36	1	509	56	dom all sizes
SM-26*	2117	SW	2	160	0	668	86	12	85	700	91	few to none
SM-27*	2090	NNW	2	250	0	464	48	23	15	133	50	bell shape
SM-28*	2084	NE	4	85	0	372	92	3	90	0	0	few to none
SM-29*	2074	NNE	5	200	0	700	41	50	16	605	79	bell shape

Table 4 continued.

Site	Elev (m)	Aspect	Slope (°)	Stand Age[1]	Fire[2]	Density of Live Trees trees/ha	Density of Live Trees % pinyon	Total Basal Area BA(m^2)/ha	Total Basal Area % pinyon	Density of Dead Trees logs/ha[3]	Density of Dead Trees % pinyon	Juniper Distribution[4]
SM-30*	2067	NE	2	70	0	113	100	5	100	0	0	none
SM-31*	2052	NW	2	65	0	95	0	8	5	191	83	few all sizes
SM-34*	2117	NE	2	120	0	987	87	12	83	382	100	few to none
SM-36*	2088	N	2	90	0	95	100	1	100	32	100	none
SM-38*	2152	NW	17	300	1	637	45	39	24	446	71	some all sizes
SM-42*	2114	NNE	1	330	0	637	55	26	45	318	100	some all sizes
SM-43*	2091	E	5	210	0	223	86	3	96	286	89	few sm sizes

* indicates additional plots with 0.5 km spacing sampled to study the pattern of pinyon pine invasion into sagebrush communities.
1. Stand ages were estimated using piñon pine samples only.
2. Includes standing dead trees and cut stumps.
3. Generalized shape of juniper frequency distribution. p = piñon, dom = dominates, lg = large.
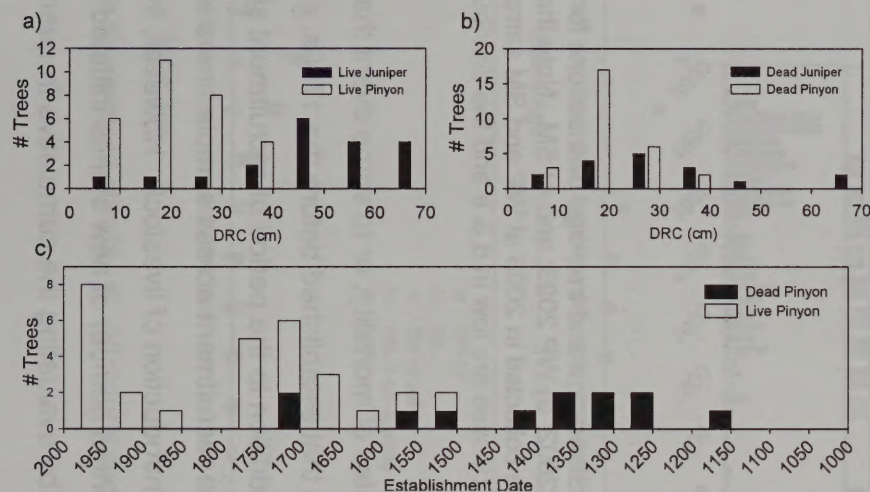
Figure 10. Size- and age-structures for trees at site GG-102. a) Distribution of 10 cm diameter classes for live trees; b) Distribution of 10 cm diameter classes for dead trees; c) Distribution of 50-year ring-count classes for live and dead piñon pine trees. Though not shown, the life-span of dead trees overlaps with establishment of living trees.

Figure 11. Stand-age and tree-age distributions for sites in each sampling unit. a) DWSA; b) GG; c) WP 2002; d) WP 2003; and e) SM. Note that only 2-6 cores from the dominant size classes were collected in 2003 at WP and SM sampling units (d & e). Thus, the frequencies for all tree-age classes are low in d & e and the distribution and the younger tree-ages are truncated.

or lower rates of mortality, or to some event that caused the mortality of most of the individuals that established before the 1700s.

In addition to the period of recruitment starting 250-300 years ago, there is a peak in tree recruitment across sample areas at 80-120 years (Fig. 11 b-e), which post-dates the introduction of livestock. However, this is not a period when an unprecedented number of new stands initiated. Patterns of stand initiation can be compared by evaluating the cumulative frequency of stand ages from the establishment

of the oldest stand until the present. If there is a time period where an unusual number of stands initiated the cumulative age-frequency curve would have a notable increase in slope. On the other hand, if stand initiation is fairly constant through time, one would expect the curve to have a constant slope. When the whole landscape that was sampled is considered, the cumulative age-frequency curve for all stands combined is nearly linear between 100 and 500 years of age (Fig. 12a).

There are different patterns of stand initiation among the 4 sampling areas (Fig. 12b). Fewer stands were sampled in the DWSA (n=23) and GG (n=20) areas than the other two areas, and stand ages tend to be older in those locations as well. The curves level off about 150 years ago.   In the SM sampling area, plots were located closer together in the invasion zone (between 2000 and 2100 meters elevation, Fig. 7), yet this bias did not cause a change in slope around 1880 relative to previous time periods (Fig. 12b). In fact, were these extra stands to be excluded, the curve for Sims Mesa levels

a)

b)
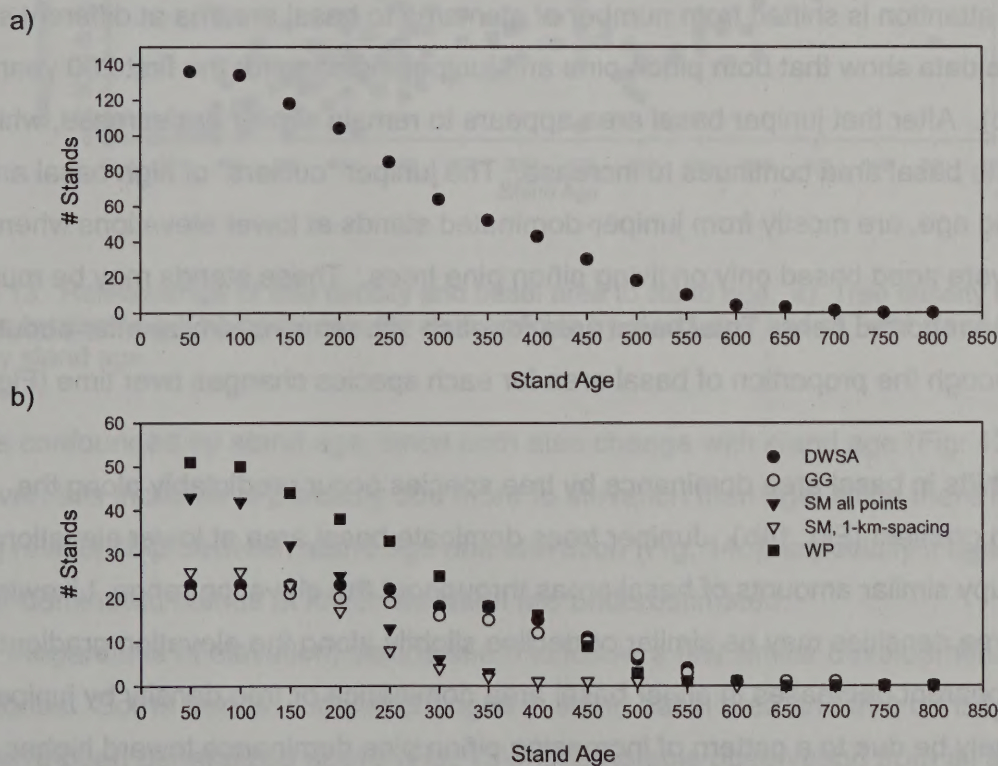
Figure 12. Cumulative Age-Frequency curves for sampled stands. a) All stands combined; b) Cumulative frequency by sampling units.

off between 150 years ago and the present, with a shape more similar to that seen at the other three sampling areas.

Because sampling methods varied among case studies, structural information is presented as number of units per hectare to standardize results. The densest stands had more than 1000 tree-stems/ha (Table 4: DWSA-N1, -N6, -S5, -S6; GG-1039; WP-1a, -2, -15, -53, -87, -88, -107,- 108, -126; SM-57, -58, -68, -53). Only two of those stands are less than 150 years old, and seven are older than 300 years. The youngest stands were not the densest stands. Comparison of tree densities by site to estimated stand ages suggests that piñon pine may increase in a stand until about 200 years, but then decline (Fig. 13a). The data suggest a second increase in piñon pine stems from about 300-400 years followed by another decline, and possibly a third cycle from about 500-700 years. Juniper trees, on the other hand, appear to increase steadily until about 400 years and then level off in number, or decline.

If attention is shifted from number of stems/ha to basal area/ha at different stand ages, the data show that both piñon pine and juniper increase for the first 250 years (Fig. 13b). After that juniper basal area appears to remain similar or decrease, while piñon pine basal area continues to increase. The juniper "outliers" of high basal area, but young age, are mostly from juniper-dominated stands at lower elevations where stands were aged based only on living piñon pine trees. These stands may be much older than reported here. Total basal area for each site remains similar after about 250 years, though the proportion of basal area for each species changes over time (Fig. 13b,c).

Shifts in basal area dominance by tree species occur predictably along the elevation gradient (Fig. 14b). Juniper trees dominate basal area at lower elevations, but can occupy similar amounts of basal areas throughout the elevation range. Likewise, juniper tree densities may be similar or decline slightly along the elevation gradient (Fig. 14a). Apparent decreases in either basal area dominance or tree density by juniper may largely be due to a pattern of increasing piñon pine dominance toward higher elevation. The relationship between elevation and either tree density or basal
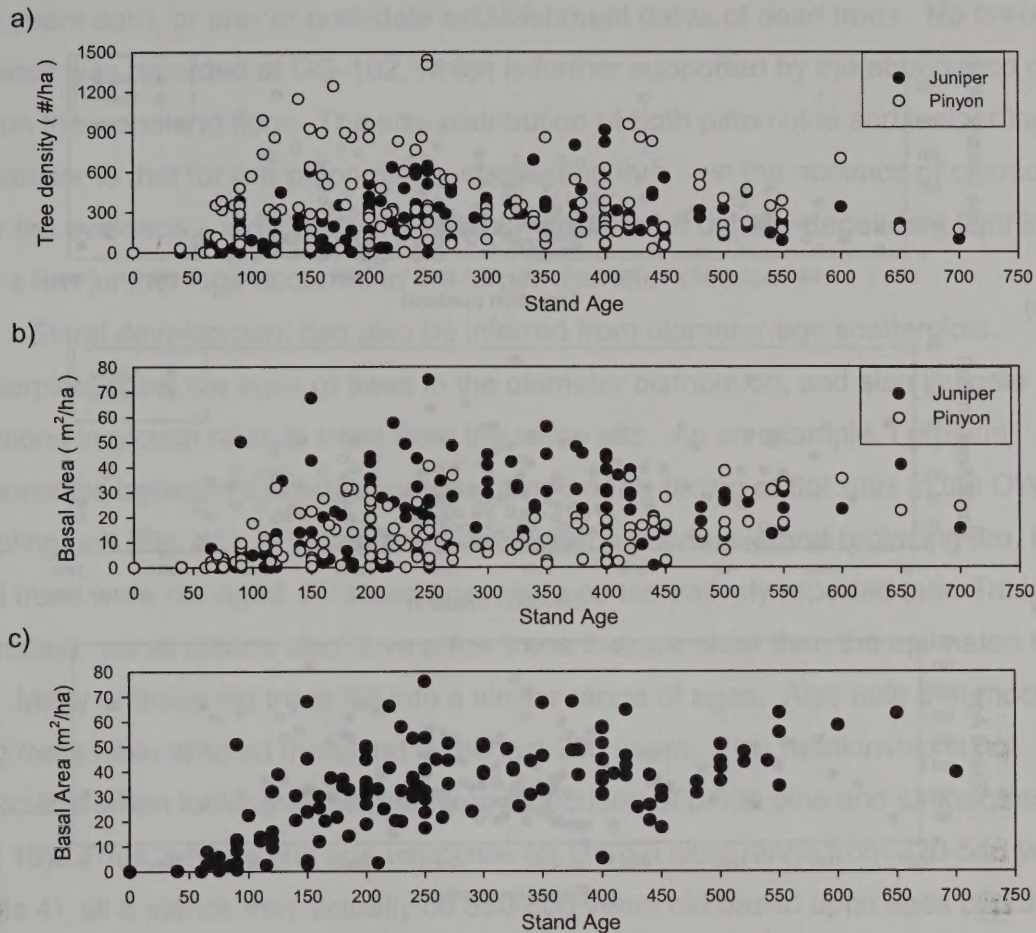
a)

b)

c)

Figure 13. Relationships of tree density and basal area to stand age. a) Tree density for each species by stand age; b) basal area for each species by stand age; and c) Total stand basal area by stand age.

area is confounded by stand age, since both also change with stand age (Fig. 13). However, this increase is probably due more to elevation than age, since there is not a strong relationship between stand age and elevation (Fig. 14c), especially if ages of juniper-dominated stands at lower elevation are underestimated.

Regardless of elevation, stands seem to follow a few similar developmental trajectories. Some trends, such as changes in stand basal area and tree density over time have been generalized above (Fig. 13). One notable observation from all sampling units is that the size distribution of trees within a stand does not mirror the age distribution. As an example, site GG-102 (Fig. 10) shows a normal-shaped distribution
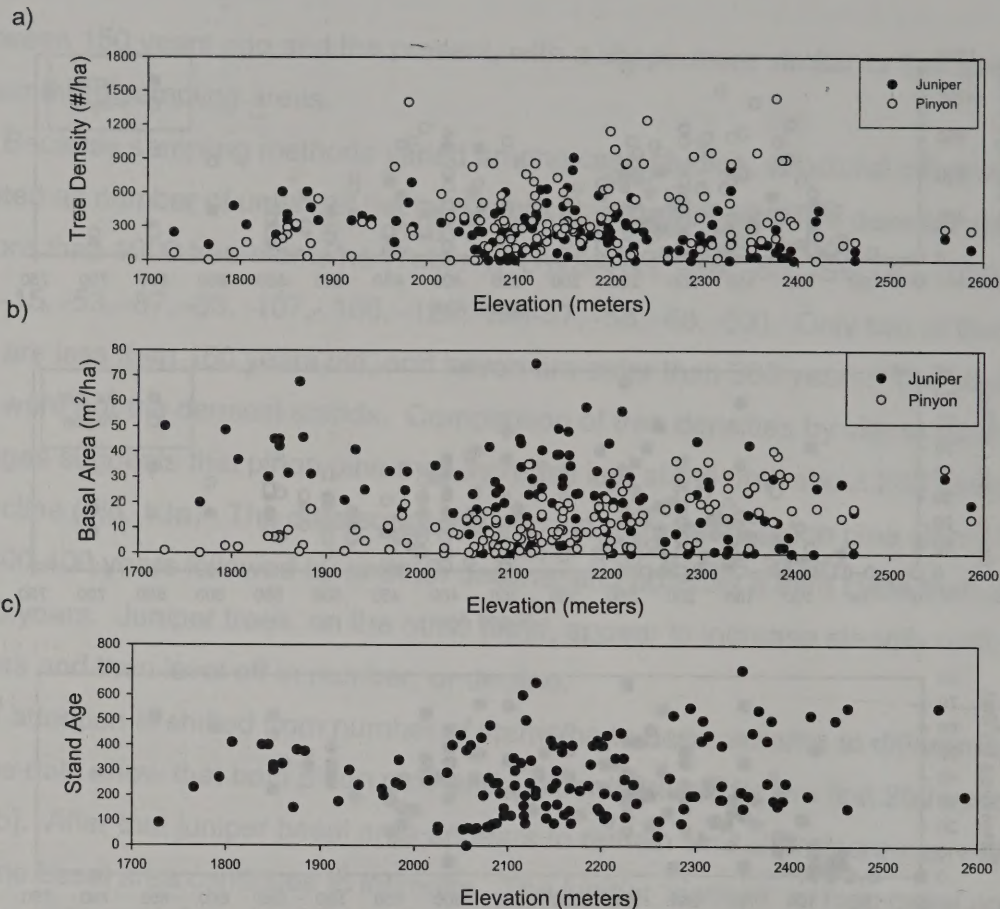
Figure 14. Relationships of tree density, basal area and stand age to elevation. a) Tree density and elevation by species; b) basal area and elevation for each species; and c) Elevation of stands of different ages.

of piñon pine diameters and a skewed distribution of juniper diameters, with more junipers in the larger classes. Establishment dates for piñon pine trees at GG-102 (considering both live and dead trees) suggest that recruitment began much earlier than dates of living trees indicate. Live trees date back to about c. 1500, with peaks in establishment from 1650-1750 and 1900-1950. Establishment dates for dead trees appear to begin about 800 years ago; mortality dates could not be determined because of erosion of the sapwood. The life spans of live and dead trees in this plot overlap (data not shown), suggesting that the establishment of dead and live trees in this stand are continuous and that the dead trees are not remnants from the previous stand. Large juniper trees may share establishment dates with dead piñon pine trees (c. 1200-

1350 years ago), or pre- or post-date establishment dates of dead trees. No fire evidence was recorded at GG-102, which is further supported by the abundance of old logs on the woodland floor. The size distribution of both piñon pine and juniper logs was similar to that for live piñon pines, suggesting that – in the absence of charcoal or other fire evidence – most mortality is occurring through density-dependent thinning. Only a few juniper logs occurred in the larger diameter classes.

Stand development can also be inferred from diameter-age scatterplots. Scatterplots show the ages of trees in the diameter distribution, and also indicate variations in growth rates in trees from the same site. As an example, I present relationships between diameter and age from 8 north-facing or flat sites in the DWSA sampling unit (Fig. 15). All sites had evidence of a previous stand-replacing fire, but dead trees were not aged. All stand ages were conservatively reported (see Table 4 for estimates), yet all stands also have a few trees that are older than the estimated stand age. Many of these old trees fall into a similar range of ages. Also note that most of the living trees have entered the stand in the last 250 years. This relationship is not predictable when looking at the diameter distribution of piñon pine and juniper trees (Fig. 16). Thus, while stand age estimates for DWSA sites range from 220-540 years (Table 4), all 8 stands may actually be 550-600 years old based upon ages of old trees (Fig. 15), juniper size distributions (Fig. 16) or both. This observation is further reflected over the entire DWSA landscape, which suggests an increase in tree density in DWSA 260 years ago, and an earlier change in tree density starting 520-550 years ago (Fig. 11a).

A similar pattern occurred in sites that were dominated by juniper trees, but where no fire evidence was found. In 5 sites from the WP sampling unit, patterns of size distribution for both tree species are similar among sites (Fig. 17). 'Age x size' distributions of piñon pine are also similar among stands, with little variation in overall stand age (Fig. 18). The data show that trees with only a 5 to 10 cm difference in diameter can differ in age by more than 100 years. Like the post-fire site, the majority of trees in the non-fire sites begin to enter the stands about 250 years ago in many case (Fig. 16 c,d,e). Often discrete clumps of similarly aged trees can be identified from age-size graphs. Many of the 136 stands sampled had an 'older-larger' group whose data
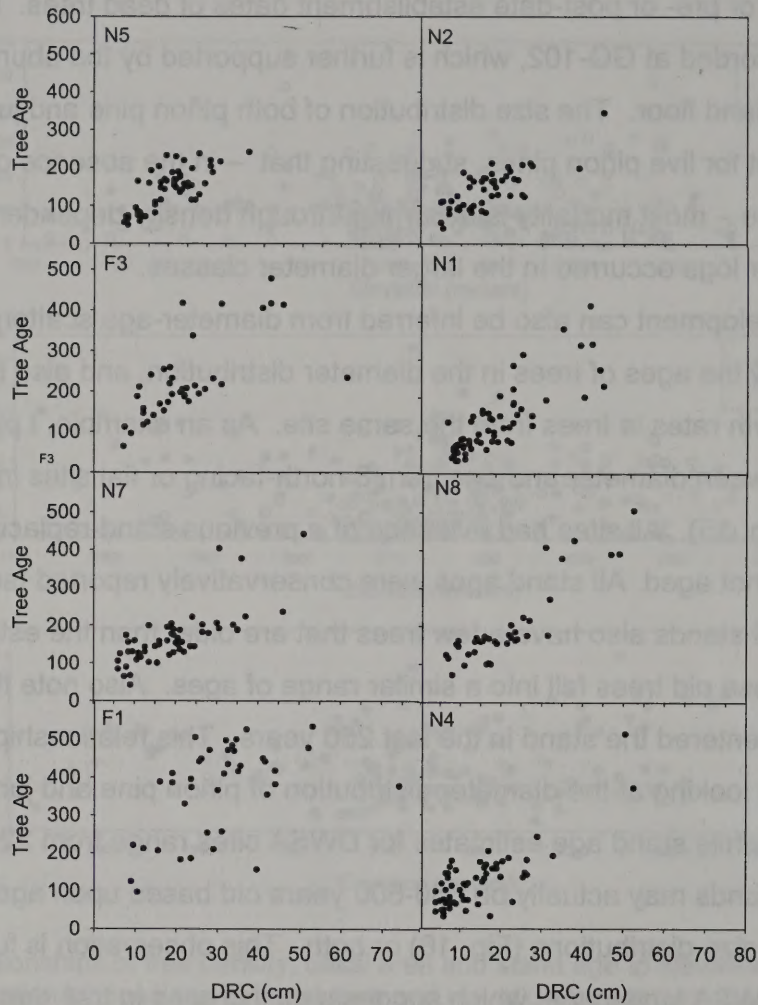
Figure 15. Relationship between diameter at the root collar (DRC) and stand age for 8 north-facing or flat sites in the DWSA sampling unit. Stands are presented in order of increasing estimated age (see Table 4).

formed a broad cloud of points, a second younger group with an age range of 100 years or less but a very broad size range, and a third younger group that tended to a linear relationship suggesting that the trees were suppressed.
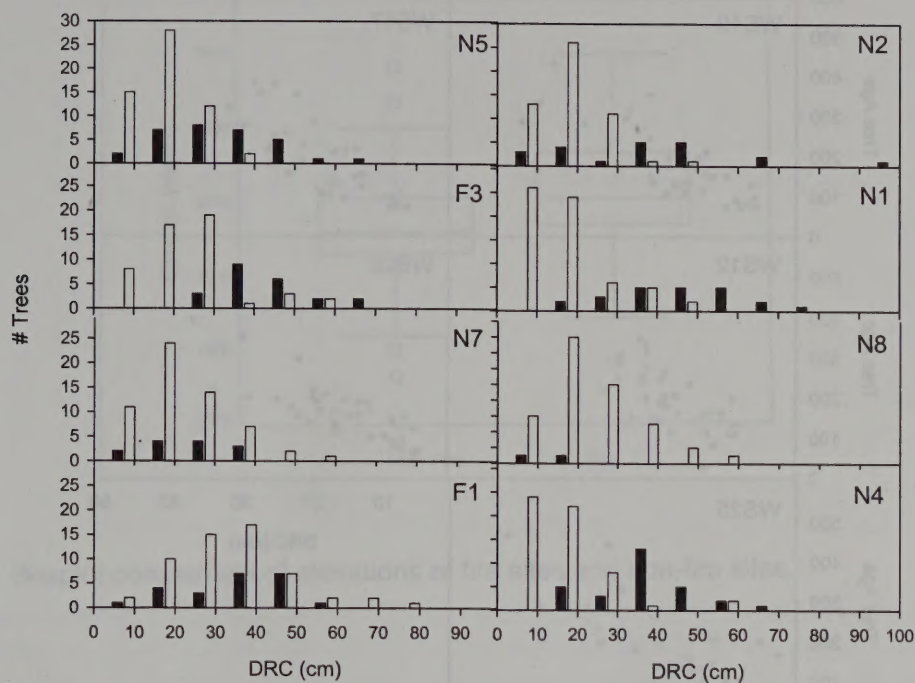
Figure 16. Diameter distributions for live trees at 8 sites in DWSA sampling unit. Stands are presented in order of increasing estimated age. ■ juniper, □ piñon pine. DRC is diameter at the root collar.
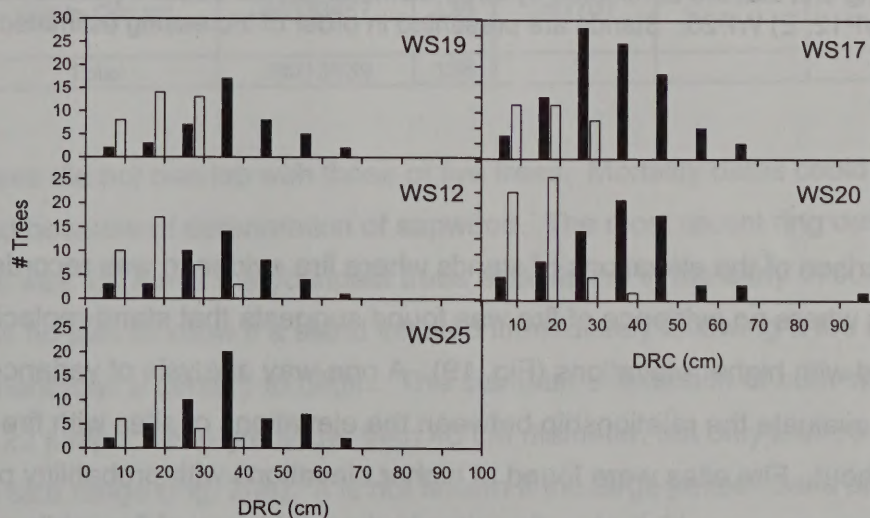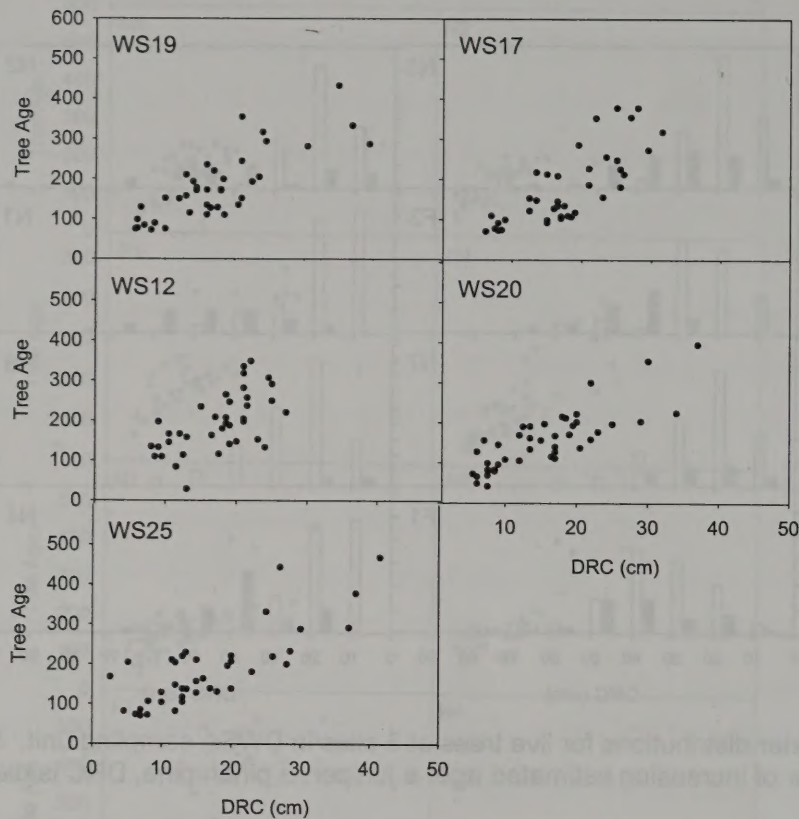

Figure 17. Diameter distributions for live trees at 5 sites in the WP sampling unit that are dominated by large-diameter juniper trees. Stands are presented in order of increasing estimated age. ■ juniper, □ piñon pine. DRC is diameter at the root collar.

Figure 18. Relationship between diameter at the root collar (DRC) and stand age for 5 stands in the WP sampling unit that are dominated by large-diameter juniper trees. A) WP19; B) WP17; C) WP20; D) WP12; E) WP25. Stands are presented in order of increasing estimated age.

Disturbance

Fire

Comparison of the elevations of stands where fire evidence was recorded versus the elevations where no evidence of fire was found suggests that stand-replacing fires are associated with higher elevations (Fig. 19). A one-way analysis of variance was conducted to evaluate the relationship between the elevations of sites with fire evidence and those without. Fire sites were found at higher elevations with probability $p < .01$ (Table 5). However, some high elevation sites had no evidence of fire, while some low elevation sites obviously generated after a stand-replacing fire.

On some sites, post-fire age structures could clearly be identified (Fig. 20b). These stands show a clear break in continuity between live and dead trees – lifespans
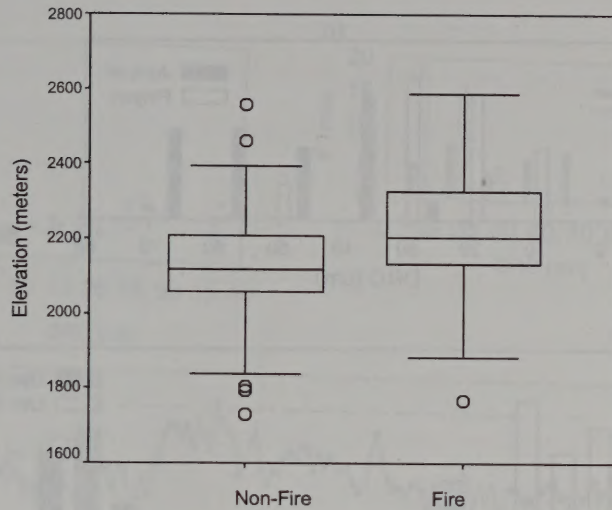
Figure 19. Boxplot comparison of elevations of fire sites and non-fire sites.

Table 5. Analysis of variance of the elevation of fire sites vs non-fire sites.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	3683471	1	3683471	14.075	.000
Within Groups	35330467	135	261707		
Total	39013939	136			

of dead trees did not overlap with those of live trees. Mortality dates could not be determined because of deterioration of sapwood. The most recent ring dated from the dead trees was 1574 and the youngest trees established in the early 1700s (Fig. 20b), but there is no way to know if a stand initiated immediately following a fire or if re-establishment took a century to begin. The diameter distribution of both species shows that 14 of 22 juniper trees are larger than 40 cm diameter, but only 2 of 19 piñon pines are in this size range (Fig. 20a). It is not known if the large juniper trees are contemporaneous with or preceded the living piñon pine trees.

Young post-fire stands had a typical age- and size-structure that can be used to characterize post-fire establishment. For example, site WP-6 was clearly a post-fire site, with fairly abundant charred logs and snags. Based on the age structure of piñon
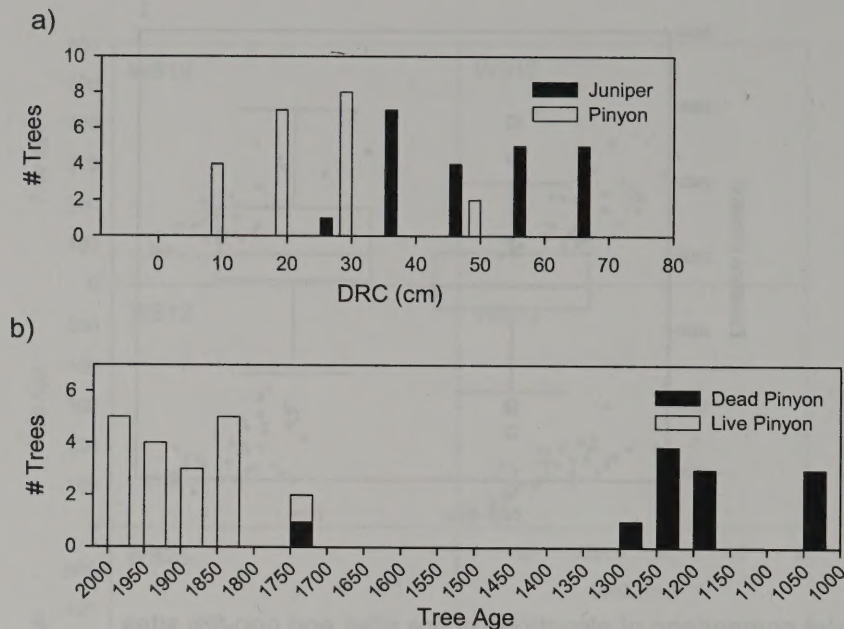
a)

b)

Figure 20. Size and age structure for a post-fire stand (GG489). a) Diameter distributions for live piñon pine and juniper trees; and b) Establishment dates for live and dead piñon pine trees.

pine, the fire occurred prior to 1820. The largest piñon pine trees were 30-40 cm DRC, and the largest juniper trees were 60-70 cm DRC (Fig. 21b). The relationship between age and size suggests that piñon pine have been recruiting into the stand at a fairly constant rate for the last 190 years, but the majority of trees are less than 100 years old (Fig. 21a). The age structure also suggests that little establishment (with survival) occurred between 100-130 years ago. Inspection of growth-indices over this time period shows below-average growth from 1870-1885, with a sustained period of above-average growth from 1903-1943 (Fig. 21c). Growth has been below average since 1996.

Comparison of the age-size structure of a post-fire stand with a young, non-fire stand shows similar establishment patterns for piñon pine. Site WP-21 has a few juniper trees in all size classes, and is dominated by piñon pine trees that are mostly less than 30 cm DRC (Fig. 22b). There are a few old trees in this site, but the majority of trees date from the turn of the twentieth century (Fig. 22a). Though there is a mixture
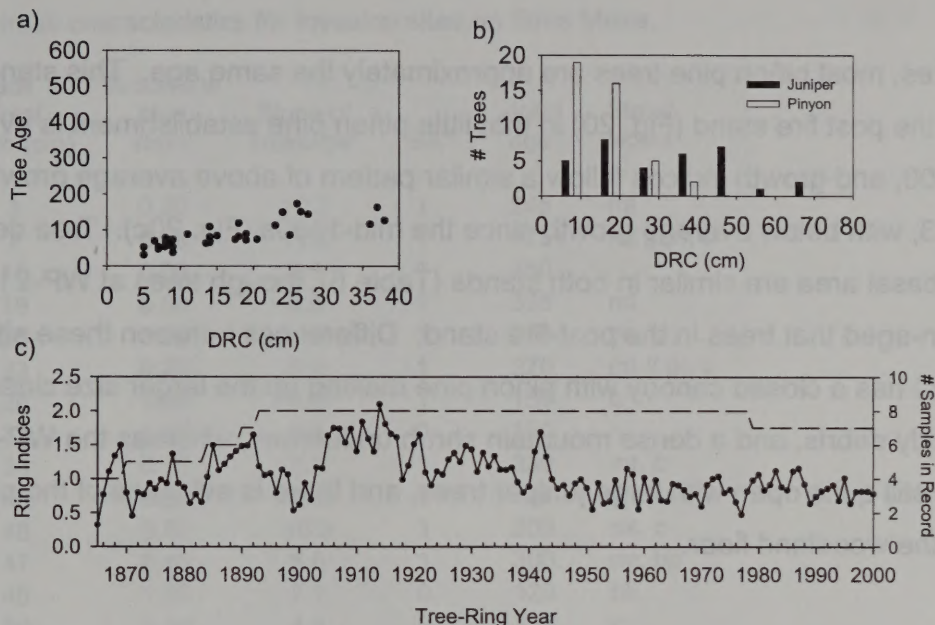
Figure 21. Size- and age-structures, and tree-ring chronology for post-fire stand WP-6. The date of the fire is unknown. a) Relationship between diameter at root collar (DRC) and tree age; b) Diameter distributions for live trees; c) Standardized tree-ring chronology showing above-average growth from 1903-1938. Scale of y-axis matches axes in Figs. 15&18.
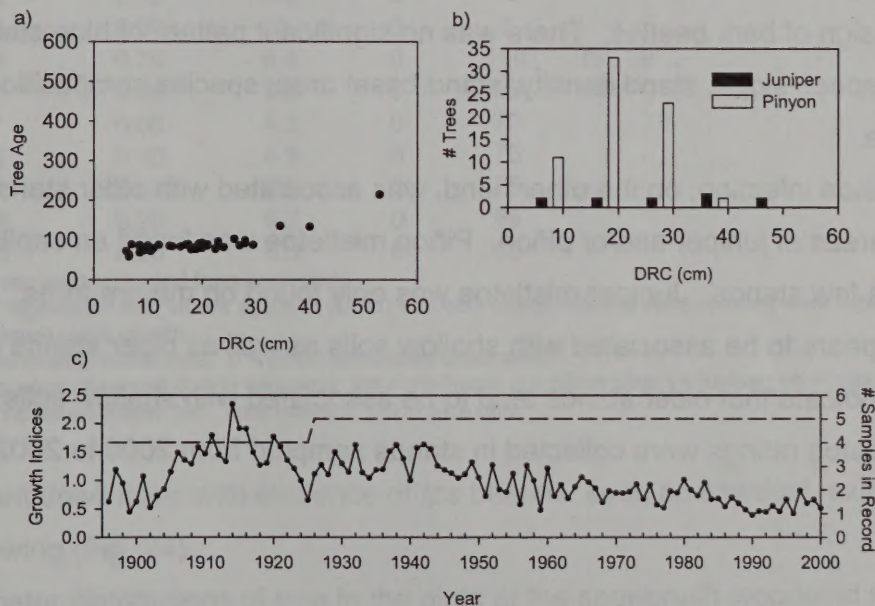

Figure 22. Size- and age-structures, and tree-ring chronology for a NON-post-fire stand (WP21). A) Relationship between diameter at root collar (DRC) and tree age; B) Diameter distributions for piñon pine and juniper trees; C) Standardized tree-ring chronology showing above-average growth from 1903-1945. Scale of y-axis matches axes in Figs. 15, 18 & 21.

of tree sizes, most piñon pine trees are approximately the same age. This stand is similar to the post fire stand (Fig. 20) in that little piñon pine establishment is evident before 1900, and growth indices follow a similar pattern of above average growth from 1903-1943, with below average growth since the mid-1980s (Fig. 20c). Tree density and total basal area are similar in both stands (Table 5), though trees at WP-21 are more even-aged that trees in the post-fire stand. Differences between these sites were that WP-21 has a closed canopy with piñon pine making up the larger size classes, scant woody debris, and a dense mountain shrub understory, whereas the WP-6 canopy is still quite open with large juniper trees, and there is evidence of the previous stand on the woodland floor.

Insects and Mistletoe

Only 7 of 76 stands sampled in 2003 clearly were experiencing an observable bark beetle infestation, yet 71 of the 99 sites sampled in both 2002 and 2003 (SM, WP, and F-sites at DWSA) had blue stain in tree cores. Many of the sites with blue stain had no outward sign of bark beetles. There was no significant pattern of blue stain with elevation, aspect, slope, stand density, stand basal area, species composition, tree age, or stand age.

Mistletoe infection, on the other hand, was associated with older stands that have high basal areas of juniper and/or piñon. Piñon mistletoe was found on saplings as well as trees in a few stands. Juniper mistletoe was only found on mature trees. Mistletoe infection appears to be associated with shallow soils as well as older stands (Table 6). This might indicate that older stands tend to be associated with shallow soils, but no soil data or mistletoe ratings were collected in stands sampled from 2000 to 2002 for comparison.

INVASION & RECENT MORTALITY

Most sites on Sims Mesa where trees are invading sagebrush also had many dead trees (Fig. 23), but cause of death was often not obvious. Many had dead buds at twig tips, and many small trees had buds ripped off of lower branches. Other stands

Table 6. Stress characteristics for invasion sites on Sims Mesa.

Plot	Soil Total depth (cm)	% cores w blue stain[1]	Slope of sizexage[2]	J:BA[3]	stand age	Stand Notes[4]
S53	3	0.20	10.3	1	245	mt
S32	7	0.00	11.2	1	125	mt (j,p), c
S27	18	0.00	7.1	1	250	
S51	19	0.80	9.5	1	325	mt
S18	20	0.00	10.4	1	250	bb, c
S19	23	0.20	9.4	1	270	mt (j,p), c
S50	26	1.00	6.8	1	150	c
S35	32	1.00	6.8	0	150	
S17	33	0.33	7.1	1	300	mt, c
S31	45	0.50	10.2	1	65	
S29	46	0.40	10.3	1	200	mt, c
S38	47	0.40	8.6	1	300	mt, bb
S34	49	1.00	7.1	0	120	bb
S33	50	0.00	4.9	0	110	c
S42	63	0.67	9.4	1	330	mt (j,p), bb
S25	21	0.00	0	1	200	c, mt (j, no p)
S36	21	0.67	3.4	0	90	
S23	36	0.20	8.4	0	75	
S43	40	1.00	7.9	0	210	bb
S30	43	0.25	6.3	0	70	
S12	58	0.00	0	0	0	
S26	68	0.75	6.4	0	160	mt, bb
S28	72	0.50	7.0	0	85	bb
S20	77	0.00	4.2	0	70	
S37	80	0.40	4.3	0	75	
S10	88	0.83	7.9	0	75	
S11	175	0.20	6.2	0	65	
S16	175	0.50	8.9	0	60	

1 Two to six cores were collected from each plot.
2   Slope (m) of regression line, where age = m (DRC) + 0; only oldest-looking trees in stand were aged. Lower slopes indicate more rapid growth.
3   1 = juniper dominates basal area; 0 = piñon dominates basal area.
4. The following were observed during sampling: mt = mistletoe; p = piñon pine; j = juniper; bb = bark beetles; c = woodcutting. If no letters follow "mt", note refers to piñon pine only.

had abundant dead trees with evidence of *Ips* beetles, such as sawdust, exit holes and audible chewing (Fig. 24).

Diameter distributions of tree in the plots at the sagebrush-woodland interface on Sims Mesa were similar. Most were composed of piñon pine trees, with the majority in the 0-10 cm DRC size class (SM: 10, 11, 16, 20, 23, 28, 30, 31, 34, 35, 36, 37). The majority of these trees are less than 100 years old. All of these sites except SM-35

have had notable amounts of recent mortality, evidenced by dead trees with orange needles and lifelike amounts of twigs and branches. Plus, all were growing in soil deeper than 35 cm (Table 6).

Tree-ring chronologies indicate the pattern of wide and narrow rings in the growth record of trees at a particular site. A tree-ring chronology developed from SM trees that are older than 125 years shows below-average growth (low ring-indices) from approximately 1878-1902, followed by a dramatic growth release that lasts until about 1930 (Fig. 25). This chronology contains 30 cores over the period 1885 to the present. Growth indices developed from trees that established *after* 1885 show rapid growth from about 1920-1950 (Fig. 25). Also, ring-widths from the 'young' chronology show particularly rapid growth from about 1983-1999 (Fig. 25). The chronology for young

Figure 23. All "encroachment" stands on Sims Mesa had obviously dying trees, but cause of death was not obvious. Many had dead buds at twig tips, and many small trees had buds broken off of lower branches. a) SM-23, ages of oldest trees are 75 years; b) SM-28, ages of oldest trees are 85 years.
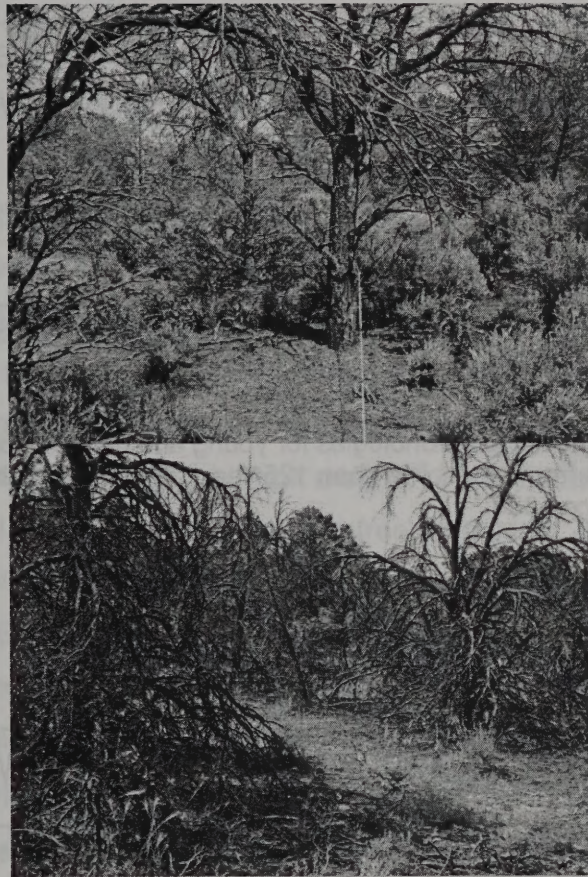
Figure 24. Young piñon pine stands attacked by the piñon Ips, *Ips confuses*. Bark beetle evidence was sawdust, exit holes and audible chewing. a) site SM-26, stand age 160 years; b) site WP-1b, stand age 120 years.

trees cannot be constructed prior to 1920 because suppressed growth in the first decade or two of most trees creates tree rings that are too small to measure.

For comparison of the SM area to other woodlands, two chronologies developed from sites in the Windy Point sampling area show dramatic release after c. 1900, which is sustained for several decades (Fig. 26 a,b). Sustained release beginning c. 1905 is typical for piñon pine trees throughout the study area. This growth pattern can be seen in the growth indices of piñon pine trees from as far away as Dolores, Colorado (Fig. 26c).
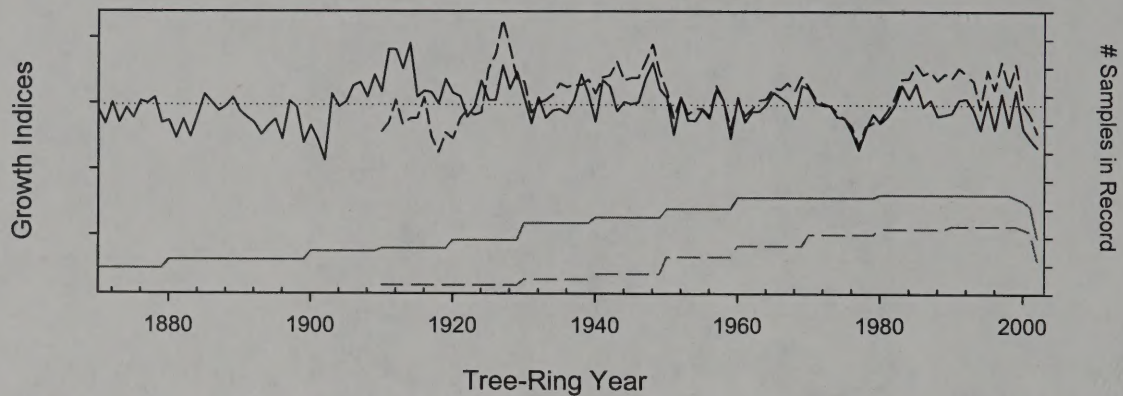
Figure 25. Standardized tree-ring chronologies for young and old trees on Sims Mesa. Heavy line shows growth indices from trees older than 125 years. Dotted line shows chronology from trees that established since 1880.
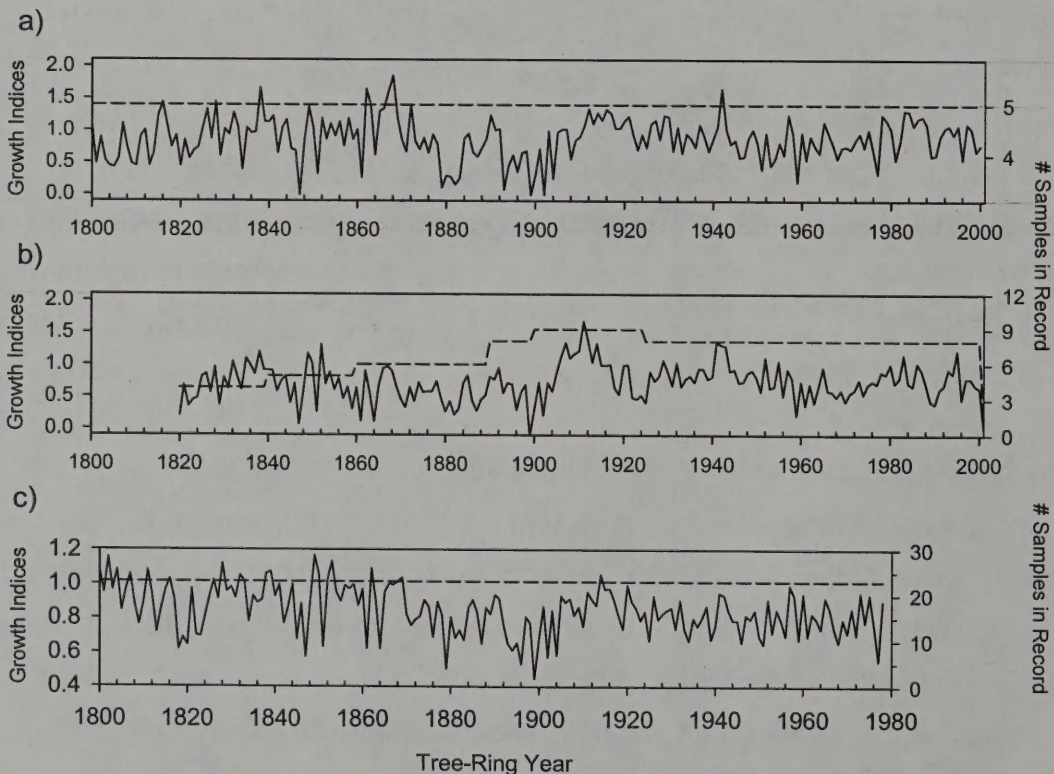

Figure 26. Tree-ring chronologies from woodland sites. A) WP-13; B) WP-21; C) Dolores, Colorado (data from NOAA 2000).

DISCUSSION

STAND STRUCTURE

Stand Age

In general, woodland stands were much older than expected. Miller and Tausch (2001) reviewed a number of studies, mostly from the Great Basin, and found that more than 90% of trees initiated after 1860. In the current study, slightly less than half of all stands were younger than 250 years, an age cutoff that Moir et al (1992) suggested for consideration as old-growth. Floyd et al (2000) and Floyd (2003) report that many woodlands in the Mesa Verde National Park area have trees that older than 300 years, with some stands that appear to have been fire-free for at least 700 years. They suggest that stands older than 400 years be considered "ancient" growth (Floyd 2003, Romme et al 2003). By these criteria, 30 of 136 sampled stands in the current study are ancient growth and 53 are old growth.

No one particular factor can account for the location of young or old stands in the landscape. The youngest stands are not associated with either the upper or lower ecotone, though they can be found in these positions. Old stands were not restricted to steep, rocky slopes and occurred on both thin and moderately deep soils (deeper than 45 cm, see Table 8 for SM area data). Observation of log debris in old treatment sites suggested that many of these stand, though occurring on flatter sites, were old-growth stands at the time of destruction. This is not what I expected, based on frequent allusion in the piñon-juniper literature to invasion of trees into deeper, finer-textured soils and into ecotones. I expected to find the oldest stands limited to sites of low potential productivity.

Increases in Tree Density

Surprisingly, the youngest stands were not the densest stands, even though the piñon-juniper literature frequently suggests that encroachment and increased densities have come as a result of fire exclusion since c. 1880. Though density does appear to be related to stand age, the relationship is cyclical rather than linear (Fig. 13). Piñon

pine density increases to a maximum in young stands (< 250 y), then decreases due to competition or other factors, only to increase again as old trees die and resources become available for a new cycle of recruitment. Increases and subsequent decreases in tree density may occur through internal stand dynamics that govern establishment and mortality, or could be controlled by external disturbance events and/or climate. The length of cycles of increasing density and stand thinning probably vary by site, but multiple stands might be synchronized by regional climate. In stands on more stressful sites, tree establishment may not lead to canopy closure, but density-dependent thinning still occurs on these sites and probably indicates that underground resources are fully utilized. On sites with higher productivity, density-dependent thinning is evidenced by a fairly uniform distribution of tree stems (Fig. 8) with little herbaceous or shrubby growth in the understory. Because of wide variation in tree densities with age and on sites of different potential, density is not a useful indicator of stand age or stage of development.

The early 1900s are a period of rapid change in tree density for many sites on the Uncompahgre Plateau (Fig. 11 b-e). When you compare establishment dates for all trees, there is a pulse of new stands as well as recruitment of trees into existing stands within a few decades of the introduction of cattle, except in the DWSA sampling unit. Tree-ring chronologies from all sites show a dramatic and sustained growth-release that begins just after 1900. Climate reconstructions of winter precipitation (D'Arrigo and Jacoby 1991) and summer precipitation (Grissino-Mayer 1995) for northwest New Mexico show that the period from 1899 to 1904 was much drier than average, but the following decades, from 1910 to 1950 were wetter than average. The increases in tree density and synchronous increases in growth increment are coincident in time with a dramatic shift in weather from severe drought to above average winter and summer moisture.

When the number of trees that established in the early 1900s is compared to the number establishing during other periods it appears that an increase in tree density began 250 years ago or more. Longer tree-ring chronologies from the WP area suggest a general increase in growth increment during the 1800s, up to c. 1880 (Fig. 26b). Based on reconstruction of summer precipitation in New Mexico, rapid growth in the

1800s was accompanied by wetter than average weather from 1830 to 1880. Higher rates of growth-increment in the 1800s are coincident in time with a long period where rates of tree-establishment remained fairly constant across sampling areas (Fig. 11). Tree-ring chronologies are not currently long enough to compare the increase in the number of trees in the 1700s to patterns of growth. In addition, the age structures in Fig. 11 do not show establishment dates of dead trees, which are necessary in order to distinguish between a pattern that is due to improved conditions for establishment or one due to mortality of trees that established prior to the 1700s. Climate reconstructions from New Mexico show that summer precipitation was below the long-term average from 1727 to 1742 (Grissino-Mayer 1995), and this drought period followed a pluvial period that lasted from about 1608 until 1727. Thus, one explanation for the number of living trees that established after the early 1700s may be that tree density increased during wetter conditions in the 1600s, but many of these trees died in the subsequent drought in the early 1700s. Alternative explanations include a change in climate conditions that favored establishment or survival, widespread fires during the early 1700s, insect or disease outbreaks related to drought, or old-age senescence.

Pre-settlement periods of rapid tree-growth and increases in tree density suggest that more recent changes in stand density c. 80-100 years ago are not novel, and may be linked to climate-driven cycles of expansion and contraction of local tree distributions. The cumulative age-frequency diagram (Fig. 12 a) has a smooth curve with a fairly constant rate of increase between 100 to 500 years ago. However, if the ages of juniper-dominated stands were estimated incorrectly because only pinyon pine trees were aged, the shape of the curve would be more rounded than it is now. The majority of this effect would be attributable to low-elevation stands in the WP area; adjustment of affected stand ages would cause the WP cumulative frequency curve to become more similar in shape to the curves for DWSA and GG (Fig. 12b). SM, then, stands out as an area where increases in tree density since grazing may be outside of the historic range of variability. Of course, including a higher density of sampling points in an area where changes in density are suspected violates the assumption of randomness required for the cumulative-frequency distribution, which implies that all sites (and stand ages) have an equal chance of being sampled. These data suggest

that, on a landscape scale, tree density is probably not outside of the historic range of variability. However, on a site-by-site basis, there are probably areas where changes have occurred as a result of grazing or other historic management practices.

Climate and changes in tree density

Cycles of density increases and subsequent thinning may be strongly related to drought and pluvial periods. Grazing may have facilitated recruitment around the turn of the twentieth century, but the importance of grazing versus climate is called into question by the growth chronologies presented in this study. Growth-indices from stands on the Uncompahgre Plateau all show a synchronous, dramatic release that is coincident with establishment at the turn of the century. The growth release is also synchronous with chronologies outside the study area (Dolores, Colorado area Fig. 26c; northwestern New Mexico, Grissino-Mayer 1995). Regional, synchronous release suggests that climate played a significant role in stand initiation and density increases. Future research should focus on developing longer chronologies from multiple sites in order to compare growth rates and proxy climate to piñon-juniper tree dynamics across the Uncompahgre Plateau. If ungrazed reference sites could be found, it would be useful to determine whether this growth release occurs or whether the release is attributable to widespread decreases in grass-tree competition.

The tree ring record shows that conditions favorable for tree establishment and growth at the turn of the century followed a period of drought in the late 1800s. More recent drought conditions have affected the Uncompahgre Plateau since 1999, yet seedlings were encountered at almost all sites during 2000-2003 field sampling. The abundance of seedlings encountered in most plots suggests that establishment might not be limited by seed source, though climate that controls masting and favors early growth may augment recruitment.   The recent drought is apparent in the tree rings (Figs. 25,26), and also in the magnitude of mortality currently observed throughout the *P. edulis* range (Fig. 27).   Mortality, though caused by a range of agents, is facilitated by drought-induced stress. Apparently, the woodlands expanded during pluvial periods early in the twentieth century and now contract to adjust to available soil moisture during

Figure 27. Color photographs of recent drought-induced mortality south of Montrose on east side of Uncompahgre Plateau. Both photos taken November 2003.

this drought. Current biomass of trees and shrubs is out of equilibrium with moisture conditions, with impacts most likely where soil moisture is least available.

The hypothesis that tree establishment was facilitated by climate conditions is further supported by the occurrence of stand structures such as those on north aspects in the DWSA sampling area (Fig. 15). These structures are typical of many stands throughout the study area. Many stands had a handful of larger, older trees scattered through the stand. These trees often had a morphology that suggests they were open-grown (Huckaby et al 2003), and that the stand later filled in around them. The stand was more densely populated with a range of medium-sized trees whose crowns may have been touching on some sides, though overall the canopy was patchy. These medium-sized trees were more than 200 years old in many cases, supporting the interpretation that infilling began well before the introduction of livestock. Where

canopies were crowding one another, trees were self-pruning lower limbs (Fig. 8, Fig. 24 a). A peak of dead piñon in the 10-20 DRC size class was common in stands with this structure. In the GG sampling area, where dead trees were aged, the age structure of live and dead trees combined clearly supported an interpretation of density-dependent thinning with limited recruitment during this stage.

If based on only a few plots or a single snapshot in time, research from the Uncompahgre Plateau might support the thesis that the pulse of establishment since Euro-settlement was caused by grazing. There is no question that the Uncompahgre Plateau landscape has changed considerably since the introduction of livestock, and grazing may have had significant effects on particular sites. However, consideration of broad spatial and temporal scales in the Uncompahgre Plateau region suggests that the pattern of expansion is within the magnitude of increase that periodically occurred prior to the introduction of livestock. As suggested by Nielson (2003), grazing and drought conditions in the late 1800s may have acted synergistically to increase opportunities for tree establishment. However, wetter conditions following this perturbation enabled proliferation of woody species. This pattern of climate-induced contraction and expansion probably occurred periodically in the past. Thus, the effect of grazing over the entire landscape may not be so much on the tree resource as on soil condition and the potential pathways of recovery *following* disturbance. If native seed sources have been reduced by grazing and non-native species take hold, impacts on soil characteristics and loss of biotic soil crusts may limit or change the potential for recovery following disturbance or affect the potential for restoration to the historic condition. More research is needed to evaluate modern vegetation response to different kinds and intensities of natural and human disturbance.

DISTURBANCE
Fire

Fire definitely plays an important role in piñon-juniper woodlands. However, this role appears not to be frequent, low-intensity fires. Fire evidence was encountered in many stands and suspected in still more, but fire type was always stand-replacing fire.

This result is similar to what was found for Mesa Verde National Park near the Four Corners area of Colorado (Erdman 1969, Floyd et al 2000, Romme et al 2003). On the Uncompahgre Plateau, evidence of fire was more frequently encountered at higher elevation sites, possibly because these sites are slightly wetter and more productive. Also, there may be more ignitions. Many more sites with a tall, dense understory of mountain shrubs (Gambel oak, serviceberry, mahogany) had evidence of stand-replacing fire than did stands with a sagebrush understory. Lower elevation stands where productivity and ground cover are reduced rarely show evidence of any fire. Fire evidence did occasionally occur at lower elevations, but it was always evidence of stand-replacing fire.   Perhaps fire in these stands only occurs during exceptional weather conditions.

In all sampling units there were moderately abundant numbers of lightning struck trees where fire burned one or a few trees, and the point fire record also shows evidence of frequent small fires from lightning strikes (Uncompahgre Plateau Fire Plan 1999). Even within these small burns, however, nearly all trees within the perimeter are killed.   Many stands that were several centuries old still had evidence of past stand-replacing fires. The presence and size distribution of coarse woody material in some stands suggests that the previous woodland that burned may have been even older than the age of the current stand, since dead trees had larger diameters than most live trees in the stand. Lack of fire evidence in some stands might be a function of time-since-fire and size of trees prior to fire, since smaller diameter wood decays more rapidly and disappears. The actual fire date cannot be determined from charred logs because deterioration of the outer rings.

Current minimum stand ages (Table 4) clearly suggest that centuries can pass without fire return to a single location. Most sites have seen at least one interval greater than 200 years, and sizes of charred logs from a previous stand may be interpreted as a long fire-free period if charred logs have a larger diameter than living trees in the current stand. The ubiquity of the pattern of infrequent, high-intensity fires suggests that fire-suppression and fire-exclusion (through grazing) have not yet moved the piñon-juniper zone far outside of its historic range of variability when the whole landscape is considered.

Though the shape and area covered by individual stands was not determined in this study, similar stand ages did occur in adjacent sites (Figs 4-7). For example, on the upper Government Springs mesa many stands are between 170-230 years (Fig. 7, Table 6, sites SM-55 to SM-72), and most have evidence of stand-replacing fire. Other sampling areas also have a number of sites with similar aged stands that could indicate a single large fire or several smaller fires burning in a similar time period, i.e., higher-elevation sites in WP (Fig. 6). Unfortunately, exact fire dates cannot be determined. If large fires did occur, stands in some locations may have re-initiated immediately, whereas in other places stand initiation may have occurred more slowly. This would create the perception of different aged stands.

It is possible that fire size and severity varies through time for woodlands, just as has been found for ponderosa pine forests on the Uncompahgre Plateau (Brown and Sheppard 2003). The piñon-juniper landscape might periodically support very large and intense fires, perhaps on the scale of the 2003 Burn Canyon fire. If there were periods of time where very large fires occurred, one would expect a long period of time where the landscape contained a greater proportion of early-seral stages. If the time between these large and severe fires is quite long, we might expect that large portions of the landscape would be aging, so that less and less early-seral stands are present. Given long fire intervals and potentially great variation in fire size and shape, there is no reason to expect that the distribution of seral stages in the pinyon-juniper zone reaches equilibrium. In fact, the length of wet vs. dry periods in the long-term climate record suggests that rather long pluvial periods tend to be separated by 10-20 year periods of severe drought (Grissino-Mayer 1995). If fires in the pinyon-juniper zone are associated with severe drought, then the climate record argues that the potential for large wildfires is not constant through time and may increase during windows of climatic opportunity. Summer droughts in New Mexico during the late 1500s, 1780s, 1890s and 1950s were accompanied by winter drought (D'Arrigo and Jacoby 1991), and may have provided the conditions necessary for large and/or widespread fires in woodlands that share these climate patterns.

Given the long, fire-free intervals and old age of many of the stands in the sampling areas, it does not appear that the current distribution of development stages in

the pinyon-juniper zone of the Uncompahgre Plateau is outside of the historic range of variability. On a site-by-site basis there may be areas where stands are "overmature" because trees have invaded new sites. However, the tree densities in the majority of stands are not unusual when put into the longer context of a few centuries.

Post-fire stand development

Patterns of stand development do not appear to differ greatly in post-fire vs non-fire stands once a group of trees is established (Figs. 15-18, 20-22), though there were differences in amounts of coarse woody debris and composition of understories. Also, the post-fire stands tend to be dominated by large-diameter juniper trees. Many post-fire stands had tall, multi-stemmed piñon pine and juniper trees that were obviously open-grown. Non-fire stands at the upper ecotone did not have these multi-stemmed trees, though often there are a handful of larger, older-looking trees surrounded by a canopy of younger, shorter, and smaller-stemmed trees that have grown up through the brush.

Lack of charcoal in the woodland-oakbrush ecotone does not necessarily mean that the stand is not post-fire, since oakbrush also is a fire-prone vegetation type. In some places, ecotone stands had charred woody debris under the shrub canopy, and in other cases no evidence of a previous stand could be located. Post-fire establishment of tree seedlings into climax oakbrush may have been facilitated by climate patterns at the turn of the century. On the other hand, these sites may have been impacted by more intense browsing during drought conditions in the initial decades of grazing. Regardless, stand development appears to proceed similarly in non-fire and post-fire stands once a tree canopy has developed on the site.

Other Types of Natural Disturbance

Though much of the past research in piñon-juniper woodlands revolved around fire and lack of fire, other types of disturbance can influence stand dynamics. Since 200-1000 years can pass between fires, other forces obviously interact to structure woodlands. Like fire, these other influences may be closely associated with climate patterns. One kind of disturbance that periodically impacts mature stands is bark beetle

irruptions. The *Ips* beetle vectors blue stain fungus to piñon pine trees, which leads to tree death. Both the *Ips* beetle and its associated fungus are native to woodlands and persist at endemic levels in weakened and dying trees. During periods of high tree stress, populations of beetles are probably able to increase and bring about the death of a greater number of trees throughout a larger area. Blue stain was found in both young and old trees and appeared to not be restricted by tree age, stand age, stand structure or topography. Because *Ips* beetles do not attack juniper trees, they cause the basal area of affected stands to shift strongly toward juniper dominance. Past beetle outbreaks are one potential explanation for stand structures dominated by large juniper trees.

Dominance of basal area by juniper trees may be caused by several factors, however. Many post-fire studies show that juniper trees are first to colonize a burned area (i.e., Tausch and West 1988). Juniper trees then provide safe sites for piñon pine establishment. This pattern was observed on many fairly young (<300 years) sites on the Uncompahgre Plateau. In this scenario large juniper trees may be older than piñon pine trees because they arrived first. However, mortality agents that are specific to one host, such as the piñon *Ips*, may move a stand toward dominance by the non-host species (Veblen et al 1991). This also may cause juniper trees to be the oldest in a stand, and may be the case where the proportion of dead piñon is significantly greater than live piñon in a stand and the basal area is dominated by juniper trees. A third explanation for dominance of juniper trees is that they are more tolerant of drought than are piñon pine trees. Both species show evidence of partial dieback, especially in older individuals. Some sites, particular southwest-facing sites at lower elevation, are dominated by juniper trees because moisture conditions limit establishment or facilitate mortality of piñon pine trees. In this case, the distribution of piñon pine trees is controlled through edaphic processes and probably not by surface fires. Finally, juniper trees may be larger than piñon pine because they grow faster, especially in the initial cohort. Without aging juniper trees, it is not known if juniper and piñon pine are similarly aged but different sized, or if they are clearly different ages.

Very old stands, such as were found in the GG are, have size distributions of piñon pine and juniper that are similar to one another, with amounts of basal areas of

each species converging (Fig. 13b). Woody debris included a range of tree sizes of both species in various states of decay. Some logs showed evidence that they were open-grown, and may represent senescence of the original cohort. Saplings of both species were moderately abundant to rare and were released following the death of canopy trees. The structure of very old stands suggests that after several centuries piñon pine and juniper basal areas reach an equilibrium, probably maintained by gap dynamics.

Floyd et al (2003) observed that old piñon pine and juniper trees can be affected by ice storms and heavy snow loads that break off branches and contribute debris to the woodland floor. Many sites in this study also had abundant debris throughout the stand that acted both as safe sites for seedling establishment and as barriers to erosion. Other types of disturbance, such as blowdown during windstorms, appeared to be less important in piñon-juniper woodlands. Piñon pine trees are relatively low in stature and have deep taproots that help to hold them upright, even after mortality. The majority of piñon pine logs encountered appeared to have fallen because the bole rotted away from the roots. Likewise, juniper snags fall over only after significant erosion at the base exposes enough of the roots so that the tree is no longer vertically supported. The only sites where trees were tipped up with their roots intact were treatment sites. Death of trees where roots remain in the soil may help to maintain soil structure and to channel moisture to deeper storage, and may have served to maintain biotic soil crusts prior to disturbance by grazing and mechanical treatments. Pulling the roots up at tree death may have significant consequences on native soil properties and erosion.

Direct Human Disturbance
Woodcutting

It is not uncommon to find woodlands where juniper branches have been cut from trees. Juniper trees are often multi- stemmed, and most woodcutting targets only straight branches and stems. Entire trees are removed infrequently. Though woodcutting was present in all sample areas it probably had minor affects on most stands sampled in the DWSA, GG and WP sites. On the other hand, woodcutting was

quite pronounced in the Sims Mesa and Government Springs areas (e.g., sites SM-17,18,19, Table 6). Many stumps in these plots were from single-stemmed trees with relatively large diameters. Whole tree removal caused the release of piñon pine saplings and contributed to the current increase in piñon density. Based on stand development throughout the sampling areas, this was an unusual pattern. Stand reconstructions suggest that it is more typical for piñon pine rather than juniper to be impacted by selective disturbance agents. Removal of entire juniper trees affects local seed supplies, and may tip species composition even further toward piñon pine. Sites where substantial juniper biomass has been removed may be outside of the natural range of variability.

Treatments

The sampling grid at SM was often interrupted by old and recent treatments. Treatments are restricted to flat or gently sloping sites by the heavy equipment that is used. Cursory inspection of many old treatments showed tree debris that was comparable in diameter to live trees from sampled stands. Indeed, many sites on Government Springs and the upper Sims Mesa were restricted to the perimeters of old treatments because of the ubiquity of human disturbance. Clearly many of the affected stands were not decadent growth that initiated following grazing. If the SM area is indicative of a similar pattern across the Uncompahgre Plateau, management actions have had a disproportionately negative effect on old-growth woodlands, especially on sites with gentle slopes.

On the other hand, where woodlands have re-established in some treatment areas, coarse woody debris may be similar in size distribution and volume to debris from undisturbed stands. Thus, combining studies of old treatments with studies of old-growth may suggest ways to restore treated stands to a more natural condition. Patterning new treatments on old growth structures as opposed to total stand destruction might provide an alternative means of improving wintering range for deer and elk. Research and monitoring would be needed to evaluate the function of novel treatments and their effect on other community components and processes.

TREE INVASION

Based on the cumulative age-frequency curve (Fig. 12) and chronologies developed from trees growing in the SM sampling unit, the increase in trees 80-100 years ago is probably not far outside of historic dynamics that may have led to high tree densities in the past. When the extra sites where sampling interval was 0.5 km are removed from the curve, the resulting pattern is similar to what is found in the DWSA and GG sampling units, with a leveling that occurs about 150 years ago. Even when these sites are included, though, the biased curve does not steepen relative to the portion of the curve older than 100 years. This suggests that past time periods may also have seen a significant addition of trees over a relatively short time period. In fact, many trees appear to have entered stands beginning 250 years ago.

Course of establishment of trees on Sims Mesa suggests that tree density might be regulated by climate, both during establishment (increased moisture) and mortality (drought). Since this increase in number of trees is coincident in time to synchronous growth release of piñon pine throughout the area (compare Figs 21b, 22c, 25-27), past "invasions" might also have come during wet periods that followed prolonged droughts, as hypothesized by Swetnam and Betancourt (1998) for the Southwest. This scenario is consistent with results from a preliminary study of fire history in ponderosa pine on the Uncompahgre Plateau (Brown and Shepperd 2003). The authors found a long gap in the fire record from c. 1780s – 1842, a period during which many of the piñon-juniper stands that are currently the densest started a phase tree establishment. As the authors point out, this gap in fires on the Uncompahgre Plateau is temporally comparable to gaps reported for ponderosa pine forests both in the Southwest and Colorado's Front Range. The Brown and Shepperd (2003) study also shows an increase in frequency and extent of fires during the early 1700s, the period that directly precedes a dramatic increase in piñon pine throughout the piñon-juniper zone. The year 1748 is one of the biggest fire years in the West (Swetnam and Baisan 1996, Swetnam and Betancourt 1998). Perhaps more or larger fires also occurred in the woodland zone over this time period. Lastly, Sheppard and Brown point out that the majority of ponderosa pine on the Uncompahgre Plateau established 100-120 years

ago following widespread fire in 1879. The timing is consistent with an establishment pulse of piñon pine presented in this report.

Patterns of establishment reported in this piñon-juniper study are also consistent with findings of Manier et al (unpubl M.S.) on shrubland cover change across the Uncompahgre Plateau since the 1930s. Those authors compared increases and decreases of tree cover over time using a time series of aerial photographs. Though they did not detect a significant increase in tree canopy over all wooded land across the Uncompahgre Plateau from the earliest photographs to the most recent, there were interesting changes to the piñon-juniper zone from one photo period to the next. They found a decrease in piñon-juniper and shrubs and coincident increase in herbs/grasses in shrublands between 1937 and 1967, and subsequent increase in piñon-juniper and shrubs with coincident decrease in herbs/grasses from 1967 to 1994. If tree density was high at the time the original photos were taken (1937) because of moister conditions beginning c. 1903 (see chronologies in Figs. 21,22,25-27), and drought during the 1950s reduced some of this dense growth, then that would explain the decrease in woodland trees from 1937 to 1967. Around 1977, a shift in ENSO activity in the El Niño phase brought an extended period of much greater than average precipitation to the Southwest (Swetnam and Betancourt 1998), which might explain the increase in piñon-juniper cover that the Manier et al. study found between 1967 and 1994. The tree-ring record from some sites (young trees in Fig. 25, Fig. 26 a,b) shows sustained growth coincident with this precipitaiton shift beginning c. 1983. If the current drought again thins woodland trees, one might expect that photos taken in 2025 will show a decrease in piñon pine and juniper trees. Given the impact of the current drought and results of the above studies, it is easy to imagine a scenario of mass mortality coincident with drought and subsequent re-establishment during ensuing wet periods (Table 9).

Mass mortality might be more dramatic in the sagebrush/piñon-juniper zone and on sites with deeper soils, since these appear to be the kinds of sites most impacted currently. Periodic pulses of mortality may be edaphically controlled. Scant evidence for any kind of fire at lower elevations reinforces a hypothesis that expansion and contraction of the lower piñon-juniper zone is controlled by soil moisture. Further

observation of the impacts of the drought and subsequent pluvial periods will suggest whether moisture availability in deep, fine-textured soils is adequate for controlling grassland/woodland boundaries.

Table 9. Hypothesized climate and tree dynamics on the Uncompahgre Plateau based on local studies.

Time period	Climate	Evidence
Late 1800s	drought	Widespread wildfire (ponderosa study), piñon pine tree rings
1900-1940s	wetter	Stand initiation for ponderosa, PJ; PJ density increases (age structures of ponderosa and piñon pine, growth indices for piñon pine.
1950s	drought	Decrease of canopy in PJ (from air photos), instrumental record
1978s-90s	wetter	Trees and shrubs recover, recruit (from air photos, growth indices Figs. 25, 26)
Late 1990s	drought	Current dieback of trees and shrubs (Fig. 27)

CONCLUSION

This study does not support the assumption that frequent, low intensity fires commonly occurred in any part of the piñon-juniper zone. Instead, the current evidence suggests that the upper piñon-juniper zone where mountain shrub species dominate the shrub layer was infrequently consumed by stand-replacing fire. This fire-regime must be taken into consideration when planning fire management activities in sensitive areas such as the Wildland-Urban Interface and utility corridors. Between fires, other dynamic processes controlled stand structure. Like fire, these processes are climate-driven. Lower elevation woodlands, with either low productivity or a more open, sagebrush understory may have burned occasionally, but may primarily be controlled by soil moisture. More research is needed to test this hypothesis. There is currently no physical evidence that frequent fires occurred there, though this may be because the evidence does not persist. When evidence was found, it was always for stand-replacing fires, which probably indicates a long fire interval of several hundred years. Post-settlement stand development on these sites will continue to alter the fire potential

unless drought impacts are able to curtail productivity. If edaphic processes are not sufficient to control woody encroachment, plans to restore a woodland structure that facilitates frequent, low-intensity fires will likely move the system outside of its natural range of variability, if it is even possible without constant maintenance.

Current structures of many older stands suggest that insect outbreaks or other selective disturbances periodically cause the death of piñon pine trees. Multi-century persistence of structures from these disturbances suggests that fire does not necessarily follow a sudden influx of coarse and fine fuels. A widespread increase in fuels across the Uncompahgre Plateau from drought-related mortality may temporarily increase the risk of high-intensity, very large fires, but this risk is probably climate driven (vs fuels driven) and likely to be present even without significant mortality under severe fire weather conditions. This fire risk, though present, is not outside of the natural range of variability. However, because fire return intervals are long, accumulation of coarse debris over several centuries may be important for some species and processes not yet studied, and this potential ecological significance must be taken into account when developing fire management plans. Landscape-wide mortality might be one natural mechanism that moves the landscape back towards a greater density of early seral stages, as is currently desired by resource managers on the Uncompahgre Plateau. If fire activity is synchronized by climate, long fire intervals indicate that the distribution of seral stages probably fluctuate over time and is most likely not outside of the historic range of variability for woodlands.

Because of naturally long fire intervals and high-intensity burns, management actions require an examination of desired outcomes and a clear indication of whether treatments are intended to reduce fuel hazard, restore natural processes, or serve some additional purpose. Fuels reduction may not be able to fulfill multiple expectations if goals are mutually exclusive. Though not yet investigated and tested, studying old-growth stands may suggest novel ways to modify stands in cases where fuels mitigation is imperative (e.g., near power lines) but restoration is not feasible. Knowledge of structural changes that occur in woodlands over time may help with the design of treatments that reduce fuels while maintaining some structural and ecological integrity. Post-treatment function of manipulated stands would need to be monitored and tested.

Alternatives to tree removal that are based on natural stand development might also be aesthetically-pleasing to homeowners near the Wildland-Urban Interface who are concerned not only with mitigating fire risk but also with maintaining viewsheds and property values.

The ubiquitous presence of old growth stands presents an opportunity for investigation into natural cycles of drought and recovery over century-long timescales on the Uncompahgre Plateau. Development of long tree-ring chronologies from different parts of the landscape may help to predict the potential for recovery from the current drought by studying impacts of droughts in the past. Long-lived trees and persistent woody debris are a natural resource for understanding landscape dynamics over a long time period. As more pieces of the Uncompahgre Plateau system are brought together there is more potential for understanding interactions and dynamics among animals, plant communities, and natural processes. In the past, woodland dynamics have been interpreted based on a short view of time because there was little material available for a longer perspective. Putting the prehistoric vegetation data together with what has been pieced together for prehistoric human populations may help us to understand and plan for the magnitudes of change that could potentially affect the Uncompahgre Plateau in the future. The long-term perspective puts recent changes into the context of natural variability, a benefit not realized by studies of woodlands in regions that lack the "old tree" resource.

This study has uncovered the importance of drought and pluvial cycles for affecting woodland communities on the Uncompahgre Plateau. When seen in light of long-term dynamics, the woodland landscape has not departed far from its natural range of variability over the last 500 years. However, woodlands structures definitely have changed in the last 150 years. The parts of the piñon-juniper landscape most likely to be outside of the historic range of variability are 1) places where a combination of woodcutting and grazing has significantly altered species compositions and physiognomies, 2) old vegetation treatments, and 3) road-impacted areas. Though not explicitly studied, roads and jeep trails were frequently encountered and often caused the placement of study plots to be readjusted. Roads serve as fire breaks, change hydrology, and act as conduits for animal movements and invasive species. Finally, I

must point out that this study only addressed the tree component of woodlands. Management practices since Euro-American settlement may have impacted woodlands and grasslands through adverse effects on soils, shrubs, and herbaceous vegetation, which ultimately affect the resilience of a site and the course of recovery following disturbance.

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